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G. Pilleri

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IN BAFFIN LAND TO STUDY THE NARWHAL (*Monodon monoceros*)

Research report by

G. PILLERI, F.L.S., F.Z.S.

Professor at the University of Berne and

Director of the Institute for Brain Anatomy.

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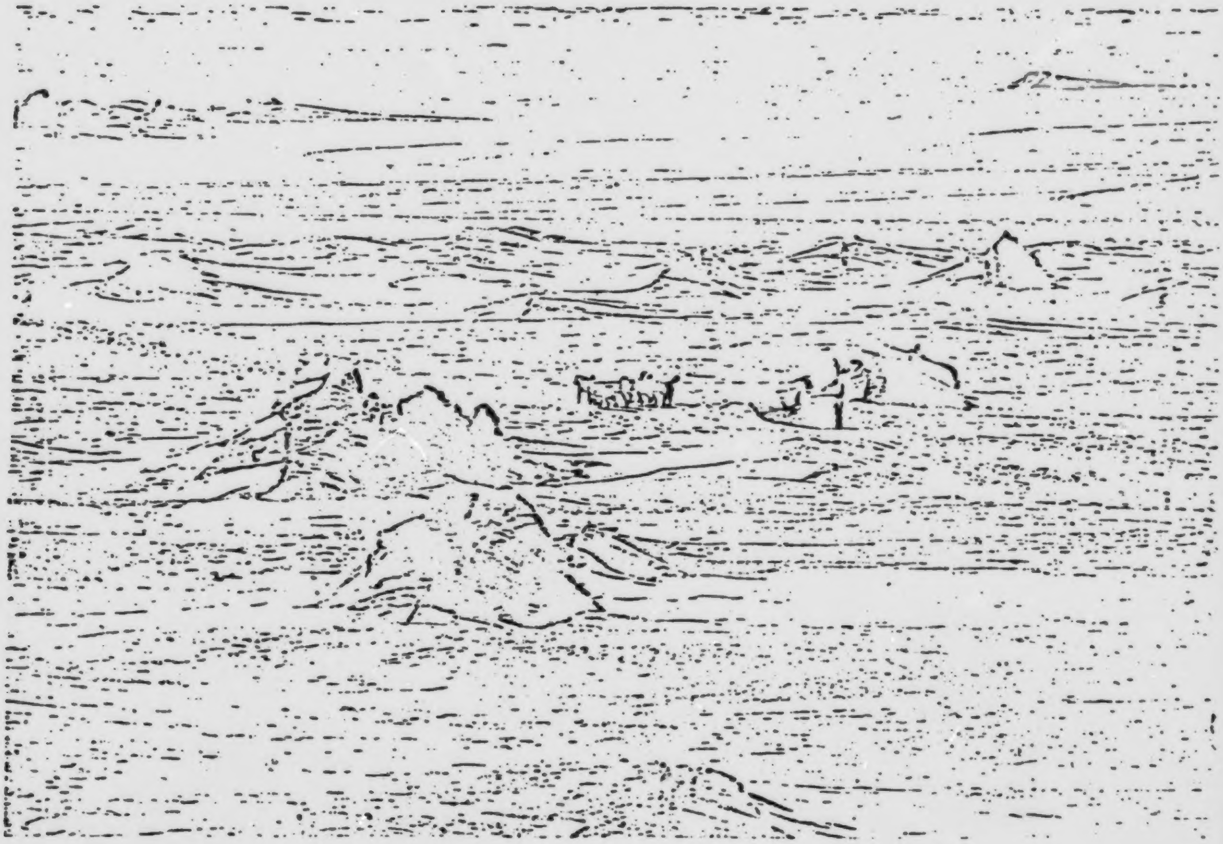
FORSCHUNGSBERICHT
VON

G. PILLERI F.L.S., F.Z.S.
PROFESSOR DER UNIVERSITÄT BERN UND DIREKTOR
DES HIRNANATOMISCHEN INSTITUTES



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Forschungsbericht
von

G. PILLERI, F.L.S., F.Z.S.

Professor der Universität Bern und Direktor
des Hirnanatomischen Institutes

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Picture of a SAVSSAT. Aquarel of F. Heimberg, 1983 (coll. G. Pilleri).

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INTRODUCTION

The major focus of my dolphin and whale studies has always been on the way in which these animals adapt in structure and function to the conditions of life in their respective niches. I spent, for instance, many years of field and laboratory work studying the blind dolphin of the Indus river, (_Platanista indi_), a species remarkable for its quite special adaptations, such as that it normally swims on its side, has marked regression of the visual organs, has twin fields of sonar emission, has extremely short sleep periods, and other special features. In order to grasp the biological interrelations between the various observations resulting from these studies, it was necessary to call upon a variety of methodologies and disciplines: in addition to morphology, the base-line study, I had recourse to bioacoustics, ecology, ethology and plaeontology. Only by such means was it possible to develop a reasonably rounded-out view of the origins of this highly evolved species which, prior to my studies, even the experts had considered to be primitive.

There are, in addition to Platanista, other unusual cetacean species -- for instance the sperm whale and relatives of Hyperoodon-- none of which has, as yet, been thoroughly inve[illegible]igated. But no species is quite so unusual as the narwhal, which lives North of the Polar Circle; nor has any species so stimulated the curiositiy of cetologists and laymen, alike. So far, even today, the hard-to-reach narwhal which, for centuries, was considered to be the fabled unicorn and was highly prized in the pharmacopoeias of the Middle Ages and the Renaissance because of the healing power of its miraculous tusk, has lost nothing of the mystique and might of its own North Polar Seas. Nor is it at all certain that research will be able to discover the true nature of this creature: quite a few mammals have been eliminated by humans before scientists could study them more closely. Ivory is today once again in great fashion, and the narwhal provides ivory of the highest quality.

Once upon a time, narwhal-tooth was a miracle drug, worth its weight in gold; today, it is just as much coveted by souvenir hunters and jewellers. It is difficult to estimate the number of narwhals killed each year to satisfy these needs.

Nominally, catch-quotas (5 narwhals per Inuit hunter) and the animals actually killed, are under the control of the authorities in the hunting preserves of Canada and Greenland; but the hunt with kayak and harpoon is a thing of the past, and has been replaced by the hunt with high-powered rifle and fast motor boat. It may frequently happen that a hunter only wounds his prey and then looses it among the ice floes. Animals that die in this way escape the official tallies.

In this situation, the modern biolgist and environmentalist are suddenly faced with so many, quite new, questions -- some of which even become involved in politics -- that they are rarely able to find appropriate answers on their own.

Though much has been written about the narwhal, our knowledge of its natural history is still full of lacunae. Furthermore, it has not been possible to maintain this animal for prolonged periods in an aquarium, as other cetaceans have been kept. We know very little about either its behaviour or the social structure of its herds. Reports concerning the narwhal's migrations and winter habitats are exceedingly sparse and uncertain; the real size of the population is undetermined; we know next to nothing about its physiology and nervous system, and but little about its sonar echolocating. The shape of the sonar field it beams out has only been calculated from a theoretical basis; the significance of the long tusk and its spirals are shrouded in mystery. In short: what are the specific morphological and functional adaptations of the narwhal to its special environment -- an ocean covered over by ice? Biologists, so far, have not asked themselves these questions.

Canada has carried on narwhal research programmes for over ten years. One group of biologists works with Dr. A.W. Mansfield in Montreal, at the St. Anne de Bellevue Arctic Station; another, under the leadership of Dr. R.W. Moshenko, at the Fresh Water Institute in Winnipeg. Finally, there is a third group, working in Vancouver, partly at the aquarium, partly at the University's Zoological Institute. Those, by themselves, are impressive numbers of professionals who concentrate their work on a single species of the cetacea, and one might expect that the goals they have set in their programmes may soon reach fruition. So far as I can see, their interests -- except for the Vancouver group, which conducts basic research -- center on acquisition of quantitative data (age, sex, distribution, reproductive rate, etc...) for the population of all of the North West Territories, to protect that valuable animal effectively. This is difficult, partly because of its vast range, partly because the hoped-for narwhal protection inevitably conflicts with the interests of the local (Inuit) hunters. Ever since the value of ivory has been increasing in the market place, the hunters have demanded constantly increasing catch quotas. Even though in the United States the importation of narwhal tusks is legally prohibited, it is still permitted in Europe. The situation is further complicated by ethnic and political considerations, such as the independence of the Inuit and the legal ownership of the arctic hunting and living ranges; ever since more and more mineral wealth is being discovered in the Canadian Arctic, the problems are becoming increasingly acute.

I had been thinking about the narwhal's bodily shape for several years, but work on the river dolphin had precedence. It was not until the summer of 1982 that I was able to travel to the Arctic, to Baffin Land, in order, first of all, to collect anatomical specimens and preliminary experience. My stay on Baffin Land was made much easier by the simultaneous presence there of several biologists from Winnipeg, who visit Baffin Land each year during the hunting season.

I am particularly thankful for the cooperation of Drs. 11
R.W. Moshenko, J.T. Strong, A.W. Mansfield and D.E. Sergeant. Special thanks also to Mr. H. Steltner; the Inuit of Pond Inlet; my travel companion, Dr. P. Maag, who all helped me in every possible way; to my friend, G. Brenner, in Vienna, for reading the manuscript and providing valuable stimuli. I should also like to thank Mrs. T. TÜscher, secretary to the Institute, who typed the manuscript. Air fare to Canada was generously financed by the Swiss National Fund for the Advancement of Scientific Research.

IMPRESSIONS OF BAFFIN LAND AND OF THE INUIT

Baffin Land, with a surface area of 476,068 km^2, is the largest island of the American Arctic Archipelago (Fig. 1). To the East it has glacier-covered, primitive rocks and a fjord-cut coast line; inland, there are an extensive plateau and alluvial plain; to the South, the coast is flat and interrupted by fjords; the West coast is alluvial. The census of 1961 enumerated 3387 inhabitants. Though poor in vegetation, Baffin Land has a rich fauna.

On July 8, I flew from Zürich-Kloten to Montreal on Air Canada. Because the connecting flight to Baffin did not leave until two days later, I was able to visit the famous Institute for Arctic Biology at St. Anne de Bellevue and to look around in the Institute for Northern Studies of McGill University. The former of these institutions arranged contacts with the Winnipeg group of biologists (Mr. J.T. Strong and his collaborators), working at Pond Inlet. The flight was continued to Frobisher Bay on First Air, then to Pond Inlet via the North East coast of Baffin Land (Fig. 1), on Nord Air. It was just at the right season: Montreal was hot and in the North the ice had begun to break up, a sign for narwhals to appear in the fjords and in the sea-lanes between the islands.

At this time of the year, American tourists bent on a fishing vacation, literally flood Frobisher Bay. The settlement was named for the famous British navigator, Sir Martin

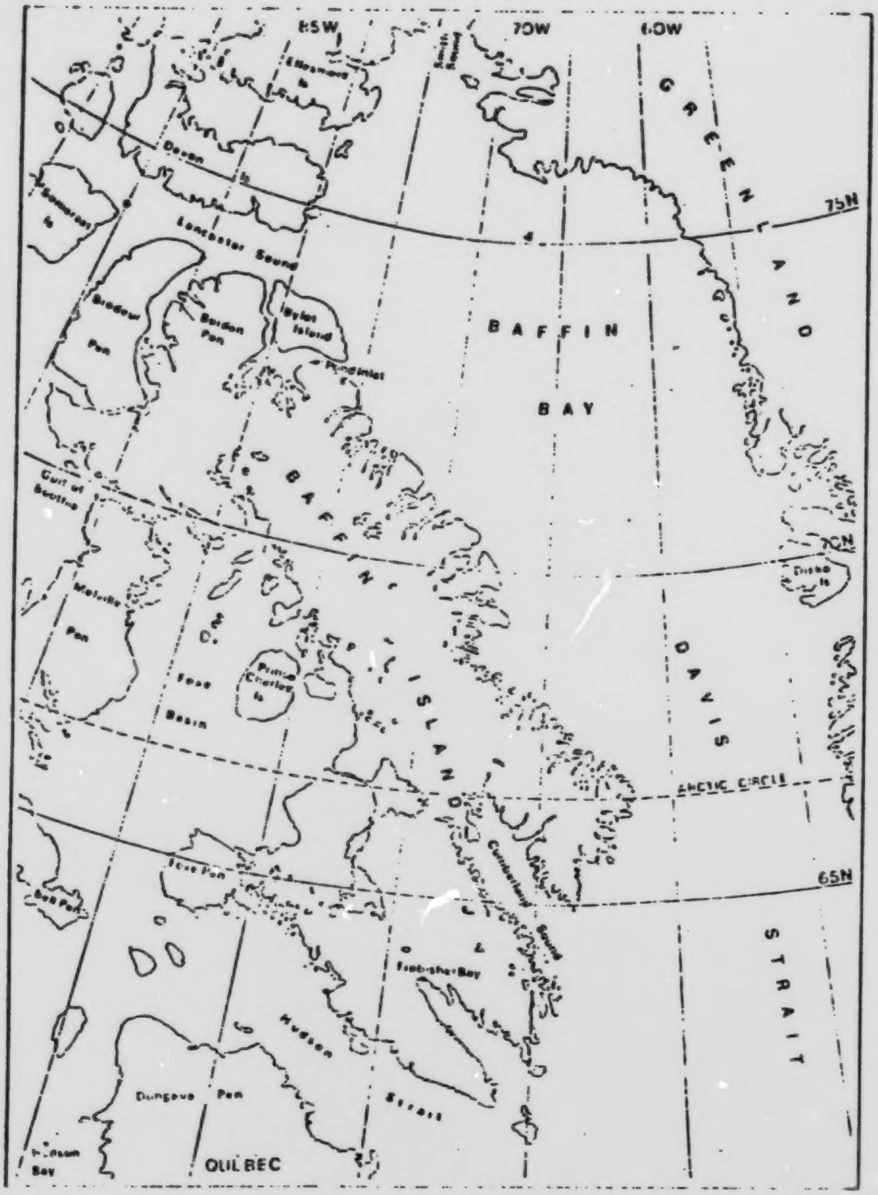

Fig. 1 Map of NWT, including Baffin Land.

Frobisher, who repeatedly visited these Arctic waters in 1577, searching for gold. Today, 2554 people, mostly Inuit, live in Frobisher. The little town, itself, however, was not founded until 1942, after the U.S. Air Force had installed a flight terminal and supply base there. From the airport one sees, in addition to low-built houses, ugly, fairly high apartment buildings which disfigure the surrounding landscape. Even the final leg of the trip, to Pond Inlet, was crowded with passengers, mainly technicians working in the mines.

Pond Inlet (72° 41'N 78° W), the "Mittimatalik" (= "there where Mittima is resting") of the Inuit, was first visited by the Polar explorer, W.E. Parry. Even though the whale (Balaena mysticetus) fishery was active in adjacent waters, the 12
Hudson Bay Company did not install a trading post -- still operating today -- until 1921. Formerly, the traditional activities of the local Inuit consisted of the huntimg seals, walrus, silver fox, narwahl and whales, and of fishing. 13
Today, all these activities have been pushed far into the background, in favor of oil exploration and mining. The economic burgeoning of the Canadian North has again provided the home environment of the Inuit with current relevance, which has entailed a simultaneous and radical change in the life style of these people. Even as little as thirty years ago, all the Inuit of the Canadian Arctic lived from the seal and fur trade. Today they live in permanent settlements, and have become dependent on paid employment and social benefits. In

just a few years, these former hunters -- who, in their own language, refer to themselves as "Inuit" (= "Human Being") -- have been forced to adapt to Western civilization.

Compulsory schooling, which was introduced by the Government, has created a gulf between children and their parents. Education confused most of the Eskimo children; they have no access to the White Man's world, and the life style of the Eskimo has become foreign to them. Modern supermarket nutrition has replaced seal and caribou meat and salmon. While tuberculosis and other contagious diseases have been largely contained, other illnesses, such as diabetes, obesity and eye diseases have multiplied abruptly. Life span and reproductive rate have greatly increased, and with them, social and ecological problems. Next to the villages there are garbage dumps of empty oil drums, Coca-Cola cans and automobile wrecks. Industrial pollution is on a still much grander scale: the Nanisivik tin mine, alone, empties 35,000 tons of poisonous substances into the ocean every year.

Living costs in the Arctic are high, three to four times more expensive than in the Canadian South. Hunting and fishing has become, today, an unaffordable luxury for most of the Inuit. A Japanese snowmobile costs Fr. 6,000(*), a plastic or aluminum boat with outboard motor, Fr. 8,000(*); ammunition

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(*) Translator's note: presumably Swiss Francs. At current (1985) rate of exchange, Fr. Sw. 6,000 = $ Can. 9,500 and Fr. Sw. 8,000 = $ Can. 12,700, approximately.

and fuel are very expensive. Because of these conditions, the Inuit are forced to catch more fur animals and narwhals, which, in turn, brings about a rapid decimation of these animal populations. No one can tell today what methods will provide an escape from these miseries.

In 1970, "Tapirisat", an Eskimo Brotherhood, was founded as the supra-regional representative body of Canadian Eskimos, with the mandate to examine the history of land use from the first days of annexation to the present, and to determine who is the legitimate owner of the land. The motto of this Eskimo Brotherhood, which was founed in 1970, is "we must determine our future ourselves". But when one considers today's political and economic development in the Canadian North, such goals appear difficult to reach.

Arctic Canada is now known as the great raw-materials repository of North America: gold, silver, uranium, zinc, asbestos, lead and oil are all hidden there. Giant projects, such as those of Petro-Canada, plan to transport, among other things, liquified gas in super-tankers from the High North through the Davis Strait to ports in southern Canada. Both the Inuit as well as the Canadian Arctic Resources Committee have serious misgivings about these projects. They would open up 14
14 areas which are among the last hunting territories of the Inuit, and where seals and walrus, caribous and musk-ox, polar bears, salmon and immense bird populations still exist. Some

40% of the white whales living in the waters of Northern Canada, and 80% of the narwhals living there, pass through these regions during the autumn migrations. Will the Canadian Government and great administrators in the South show respect for the rights of 26,000 Inuit and the efforts the white environmentalists? Here, however, it is not only a question of respecting the democratic rights of a minority, but of preventing the permanent disappearance of one of the last of the Arctic Paradises.

Pond Inlet has a single hotel, which belongs to the Inuit Cooperative and which is extremely expensive because it has to be supplied entirely by air. Cargo vessels drop anchor here only rarely during the year. I spent just one night in the hotel; after that I moved, through the intervention of Mr. Steltner, into a small, old church which is the home of Father Guy Marie Rousselière, a well-known archaeologist, who was away on a dig.

After consultation with the biologists from Winnipeg, it was suggested that I visit an Inuit camp East of Pond Inlet, which served as a base for narwhal hunting. An Inuit family living there was just about to leave Pond Inlet, and the three biologists also wanted to move to the camp with fresh provisions. They loaned me a tent; I bought sufficient food; we left on 23 VII 1982 and made our way along the coast, where enormous ice floes greatly hindered progress. It also rained heavily. Toward the North, partly fog-shrouded, was the coastline of uninhabited Bylot Island, with its Byam-Martin mountain range. We stopped temporarily at a small Inuit camp to unload some of the supplies. Beautiful plants grew on the sparse grassy patches betwen rocks and gravel. Here and there on the ground lay whale bones and much-weathered walrus and fox skulls. Among some skeletal remains of narwhal, I found ear bones, including a well preserved middle ear with its chain of ossicles _in situ_ .

A four-hour boat ride brought us to Sadleeahrosuk, our camp (Pls. 1-3). It is situated on a broad bay, at the foot of steeply rising mountains, near the mouth of Pond Inlet into Baffin Bay. It rained all night and the following day. Using this camp as a base, I collected my materials and also made excursions into the mountains rising behind the camp. The rain continued for several days, then the skies cleared. The sunny nights are ideal for work, because there is always enough light. The European sleep cycle disappears; one eats when one is hungry, and goes to sleep, even in the middle of the day, when one is tired. Inuit children often played on the ice at two o'clock in the morning. On days of heavy rain or high wind it may happen that one spends an entire 24-hour period asleep, with small interruptions for meals. I felt no discomfort from these "hibernations". During the rain-and-wind filled days, not a sound was to be heard from the Inuit tents next to ours: all the families were sleeping.

The temperature was steady between +5 to +6 C. On some days, the sea was covered, far into Baffin Bay, with ice floes, so that no water was visible; then the ice began to move and currents pushed the entire mass into the bay. Large and small icebergs drifted by. Unfortunately, I did not have the opportunity to see and photograph swimming narwhals from shore. When a herd was spotted, two of the Canadian biologists went out and the boat was too small for me to go along. On this trip, I had to confine myself to the collection of anatomical specimens. A two-week interruption of the hunting period then forced me to return home. In spite of the relatively short stay, this first contact with the arctic environment taught me much, and the specimens I collected at the camp (nervous system, eyes, hearing organs, tusk, air-sac system, larynx, blood samples, etc...) are most useful for my studies.

THE NARWHAL (MONODON MONOCEROS) 15

a. Ecology and Behaviour

Narwhals form social groups comprising members of both sexes and juveniles, either in families of 15 - 20 animals, or in large herds of 1,000 or more individuals. These days, the latter have become increasingly rare. They are seen at the time of the great migrations, after the early-summer ice break-up, when the animals leave the pelagic regions in order to go to the shallower waters of the more southerly fjords, bays and narrows. HELEN SILVERMAN (1979) makes a distinction between groups numbering from 1 to 25 narwhals, and larger herds. Of 101 groups observed in Barrow Strait, Pel Sound and Bellot Strait, 38% were single animals and 29% pairs. The average number of individuals per group was 2.9. Such groups do not usually occur in herds (Finlay, 1976). We know their summer grounds much better than the winter ones (see MANSFIELD _et al_., 1975; TOMILIN, 1967). PEDERSEN (1930) observed these migrations yearly in Scoresby Sound, East Greenland (page 414):

"The narwhal was a regular summer guest in Scoresby Sound. As soon as the winter ice began to break up, usually in the middle of July, the animals moved in troups into the fjord, roaming through its furthest inlets, then disappeared again into the drift-ice of the East Greenland current. Narwhals could be observed to arrive at, then leave, Scoresby Sound or the mouth of the fjord right into the month of October. But narwhals were seen occasionally also in winter at the mouth 16
of the fjord, or along the coastal ice of Liverpool Bay". From this it would appear that the migrations do not involve the entire population; furthermore, PEDERSEN reports that narwhals remain the year round at Kangerdlugsauk (East Greenland).

The deep waters of northern Baffin Bay, toward Smith Sound, and between Greenland and Ellesmere Island seem to be one of the winter quarters for the narwhal population living to the West of Greenland. This region has special physical and ecological characteristics, favorable for the marine fauna, and not yet satisfactorily explained by oceanographers.

In this, the most northerly part of Baffin Bay ("Nordwasser" [= "North Water"]), the ocean does not completely freeze-over even at the hight of winter, and so leaves open one of the many polynyas (patches of ice-free ocean) of the Arctic.

Surface temperature measurements of the North Water by means of infra-red distinctly show that the water there is warmer than further South (Fig. 2). This supports the opinions of past polar explorers, claiming that there was an ice-free, navigable sea there (see MÜLLER, 1977).

The great polynya of Baffin Bay may well represent a special feature in the narwhal's habitat, bearing some relation to the animal's migrations. In the Arctic Ocean, narwhals have a circumpolar distribution, in regions where conditions like those of the North Water, just described, are not ubiquitous. We have unfortunately no systematic studies describing the animals' winter behavior; only some chance observations. It is interesting that some of the polynyas in which narwhals have been observed are extremely small. GURBUNOV (1940) addresses this as follows: "From the shore of Scott Island we could see, in a binocular, Narwhales diving and gamboling in a small polynya, at a distance of 0.5 km from the ice edge, not only the tusk, but also the head and part of the trunk constantly emerged from the water". PORSILD (1918) remarks: "the small holes which the ice-bound animals keep open have a special

Eskomo (sic) name: savssat. Their area sometimes does not exceed 30 - 100 cm in width and a few meter (sic) in length. The Eskimoes (sic) easily find such animals by their spouts and easily kill the entire group from the ice". These observations are also confirmed by NANSEN (1898; p.97): "Sunday, 19 May. The surprise the "seventeenth" brought us was nothing less than that we found the surrounding channels full of narwhals. Just as we had begun to get under way and were about to cross the crevasse at which we had to make a stop the day before, I became aware of a puffing noise that sounded like blowing whales. First I thought that the sound came from the dogs, but then I heard distinctly that it cam from the channel. I listened. Johansen had, so he said, heard it all morning but had thought that it was only the far-off sound of ice being compressed. No, I believed that I really knew that specific sound sufficiently well, and therefore looked toward an opening in the ice, whence the noise seemed to come. Suddenly I saw a movement that could not have been due to the ice there; and so 17
it was -- the head of a narwhal emerged; then came the body, which described the well-known arc and disappeared again. Now a second narwhal rose, accompanied by the same sound. It was a whole herd.

... Meanwhile, the animals had disappeared from the opening in the ice where I had first seen them, but I heard them blowing from other openings further to the West. I therefore followed the channel in that direction but could not 18

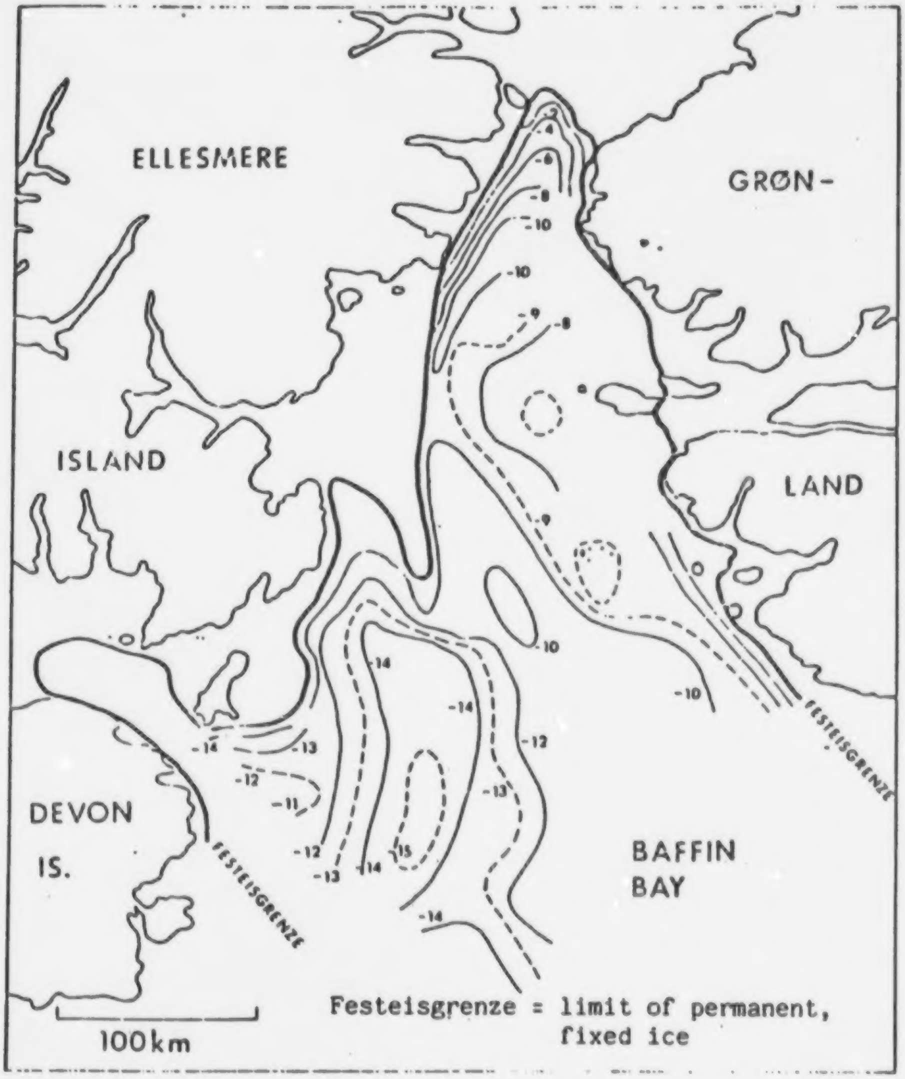

Fig. 2 The polynya of the North Water. Surface temperatures, measured in C by infra-red. Redrawn from MÜLLER (1977).

get in a shot, even though I approached the animals fairly closely once or twice. They emerged in relatively small openings, spotted along the entire length of the channel.

Thursday, 30 May. As I was standing on the high hillock, absorbed in these sad thoughts, and looked southward over the ice where I saw nothing but ridges and crevass after crevass before me, I suddenly heard the well-known sound of a blowing whale from an opening close behind me. There was the answer to my worries.

... It was a whole herd of narwhals which was taking in air and blowing incessantly.

... I stood for a long time and watched them". At the time, NANSEN'S ship, the "Fram" was located approximately at 83 N lat and 65 long.

DEGERBØL and FREUCHEN (1935) described a savssat which they observed in the winter of 1924 in Admirality Sound near Siuraqtujuk (Moffet Inlet). Six hundred narwhals were trapped in the ice and the ploynya was so small that its area had room for "barely two tents". In spite of this, none of the deeper-swimming whales injured any of those who rose into the ice-free zone. "They push and jostle their way up, carefully placing their tusk between the others". Of the catch which was made there, 203 tusks were offered for sale in Pond Inlet.

We owe the most detailed observation of a savssat to M.T. PORSILD, the former director of the Danish Arctic Station on Disko Island in West Greenland. This particular event was

observed in Disko Bay in April of 1914 - 1915, which was a 18
particularly severe winter. It happens, writes PORSILD, that
white whales or narwhals are cut off from the still open waters
of Baffin Bay, and are driven deep into Disko Bay. The frost
does not let up and the pods are concentrated into narrow or
broader, ice-free zones from which they can't escape until the
weather changes and the ice breaks up. If this does not
happen, large pods can become trapped in small puddles. When
air temperature falls to -20 to -25, condensed vapor rises from
these sites, visible from afar. When a pod of whales becomes
trapped in this manner, the expired air -- particularly if
still more animals congregate -- forms a veritable column of
steam, so that the entrapped narwhals can be located with ease
from a distance and easily fall prey to the hunters.

If a fairly small polynya is to serve as an effective
breathing-hole for a whole pod of narwhals, a majority of the
animals must stay under the ice until "it is their turn to
breathe". According to PEDERSEN (1930), the apnoeic interval
of a narwhal, at a diving depth of 300 m, is very long. For an
animal that had been harpooned, with the harpoon in its body
and dragging the float (an air-filled, leather sac) with it
under water, the apnoeic period lasted a good 30 minutes. From
this observation it becomes clear that in winter the narwhal
can spend long periods under the ice, except for short 19
intervals to breathe at the surface. No doubt, the nearly

unbroken ice-cover represents an ecological constraint sui generis which makes particular functional demands on the animal.

In addition to naturally occurring polynyas, caused by special temperature conditions in the ocean, and sought out by narwhals for breathing, there are also openings made by the animals themselves as they actively break open the ice cover (PORSILD, loc. cit.). As has been mentioned before, the narwhal uses its melon as an ice-breaker (PEDERSEN, loc. cit.). According to the observations of PORSILD (1918), the narwhal can break an ice layer 7 inches (17.78 cm) thick. Polynyas, particularly the smaller ones, are carfully kept open by the narwhals. This behaviour no doubt represents a synaporium. In crowding closely together, the animals, by their body heat, prevent the waters from freezing.

In the literature there is a consensus that polynyas inhabited or used by narwhals are real traps for the animals, from which they can not escape. That may be so -- as for other animals, too -- in particularly cold winters, but would never be the norm. Polynyas, the Inuit's savssat, are a trap for narwhals only insofar as humans can slaughter the animals with ease in the confined space.

In effect, BROWN (1868) reports: "In April of 1860, a Greenlander was travelling along the ice in the vicinity of Christianshaab, and discovered one of these open spaces in the ice, which, even in the most severe winters, remain open. In the hole hundreds of Narwhals and white whales were protruding their heads to breath (sic), no other place presentig itself for miles around".

MILLER (1955, p. 175) reports the interesting fact that narwhals use the breathing holes of seals for their own respiration. The observation came from the Inuit of Bylot Island: "The Eskimo had reported that narwhal often surface in seal holes, which are enlarged during the season by run-off of melt water from the surface of the ice. Since the largest of these holes is seldom more than fifteen or twenty feet in diameter, this seemed improbable; however, 4 females were watched for about ten minutes as they surfaced, one or two at a time, in a single seal hole which was not more than eighteen or twenty feet across. They seemed to maintain a steady rhythm of rising, heads pointed upward, then of sliding back beneath the water, and continued to surface in this fashion until we had crept to within about twenty feet of them".

In addition to the ice, light conditions of arctic winter have ecological importance. At this time of the year, day can not be distinguished from night, and on moon-lit days only is there a pale glimmer of light, which becomes reddish at night. During the time of the new moon, there is darkness. In the water, lack of light is even greater because of reflection from the ice. What effect this yearly cycle of winter dark and summer light has on the metabolism of the narwhal has not been determined. In order to orient itself in the dark, the narwhal, equipped with sonar as all the other 20
cetaceans, uses its echolocating system, and thus can do largely without the sense of sight.

"Standing" Vertically in the Water

A frequent behaviour pattern during the summer is vertical "standing" in the water, when the whole head with, in the male, the tusk, is extended above the surface of the water (Fig. 3). The animals can remain in that position for quite long periods, and the behaviour may be collective. DEGERBØL and FREUCHEN (1935) observed this behaviour at several site in Admirality Inlet: "Often they remain there apparently to avoid the killer-whale; but whatever the cause is, they will all suddenly put their heads vertically. The males with tusks let them project straight into the air, while the others merely have their heads above water, and in that position they will remain for a long time. Then all at once, likewise as if by 21
command, they dive".

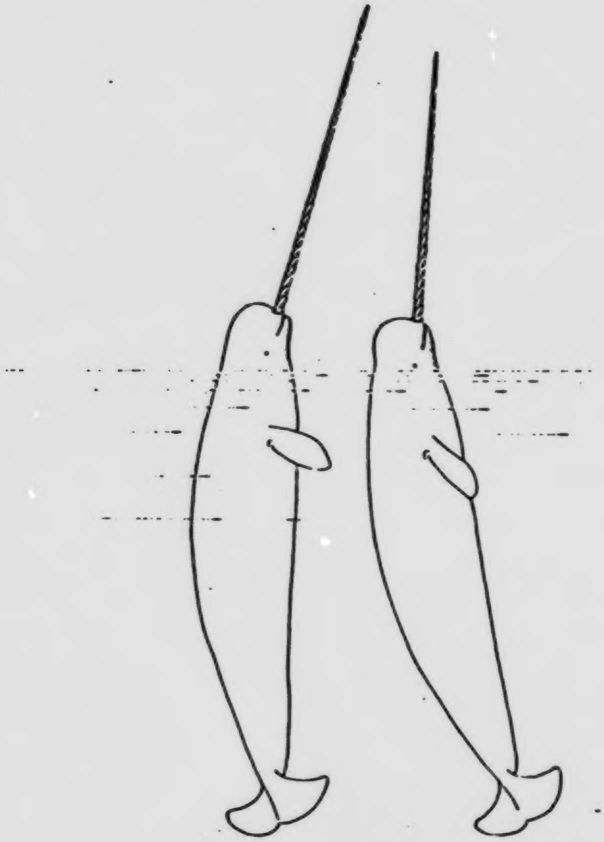

Fig. 3 . Male narwhal, "standing" vertically in the water.

They observed the same behaviour in Eclipse Sound: ... "Now and then one would raise its head vertically above the surface -- sometimes a male, sometimes a female, so that in the case of the males the tusk stood straight up. Then all at once a number of them, forty or fifty, would follow its example and do the same; and just as suddenly they would disappear".

Other toothed whales display the same behaviour, though not collectively, as the narwhal do. I have observed this repeatedly, particularly in _Grampus griseus_, _Globicephala melaena_ and _Delphinapterus leucas_.

Rolling Around the Body Axis

Another attitudinal movement is rolling about their own body axis. DEGERBØL and FREUCHEN (loc. cit.) observed this also in the warmer season (July). They describe the behaviour pattern as follows:

(p.259) 5 July. ... "And it became clear that the narwhales had been chased in by the killer-whale ... Sometimes they turned over in the water, so that one could see their flippers high in the air when they blew, and in some cases their tusks".

12 July (near Qaersut) ... "From a rock I had opportunities of observing them very closely. Some play, swimming round after one another. They turn their bellies upwards as they come to the surface, or show their sides"...

16 July: ... "They were below me for quite a time, sticking their tusks into the air, then running round a little in play, trying to get away from one another -- first one then [an] other leading. When they turned in the water it was always back over, as when an aeroplane loops the loop.

When turning to the side, they rolled on their side and went back over. I do not think a narwhale turns forwards over".

Resting on the Side

A third pattern of behaviour is the "lying on the side", with one flipper out of the water. The observations come from DEGERBØL and FREUCHEN (loc. cit.): "The same evening there was another school, among which several lay quite still about ten minutes at a time, lying on one side with a flipper in the air".

Sleeping Position

In the sleeping position the narwhals remain quiet for 9 - 10 minutes, with the melon out of the water, occasionally moving their pectoral fins in order to retain their balance. Sometimes they sleep with the tusk on the edge of an ice floe holding the head above water (Fig. 4).

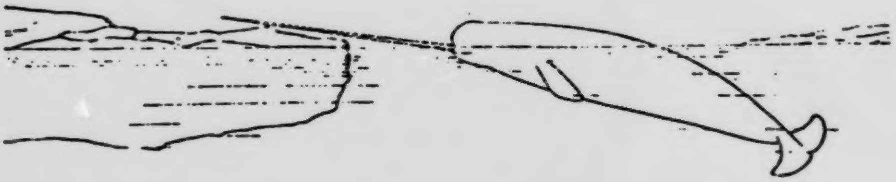

Fig. 4 Sleeping narwhal resting tusk on edge of ice floe.

Mother - Offspring Relations

This is a close relationship, and the calves remain with their mothers for a long time. When the mother is harpooned, the young animal remains close for a long while, as the following report makes clear (DEGERBØL and FREUCHEN, loc. cit.): "Today caught three narwhales, one female with a very small calf, no larger than an ordinary fjord seal. The calf swam round and round the mother and came quite close as it was being dragged up"...

b. Migrations

Our information concerning migrations is still in its infancy, confined to the statements from PEDERSEN (1930), and the works of MELDGAARD and KAPEL (1981), VIBE (1950), and GRAY (1931). The former deal mainly with relatively small, coastal locations near the hunting stations, whereas the last included broad areas of the East Greenland Sea, based on two log books of the whalers "Eclipse" and "Hope". From an analysis of the data, GRAY has determined that there is a certain correlation between the route of migration and the color of the ocean. Arctic sea water is ultramarine blue and highly transparent or olive green and little transparent. The coloration is permanent and independent of the weather. Green water occupies about 1/4 of the Greenland Sea between the 74th and 80th parallels, with only small, annual variations. Whalers refer to the areas of green water as "feeding banks" or "grounds"; they are devoid of polar water, and their waters are the first to be exposed to sunlight in the summer. The color comes from the diatoms which flourish there. This water drifts to the south-west. The narwhals which migrate to the north-east in the spring, meet the "grounds" and follow the green, moving waters; but then they turn around again and swim north-eastward towards the pack ice, which is impassable to ships. The final destination of these schools is not known.

That, however, involves only a part of the narwhal schools; others remain near the coast. There does not seem to be any separation of the sexes; the reason for the failure to migrate is still unknown. In any case, it is a fact that in their migrations the narwhals follow the green, nutrient-rich
drift-water. Narwhal migrations in Canadian waters, and size 23
of the population have so far been inadequately investigated.

"Between 21 June and 31 July 1976, scientists at Cape Hay on Bylot Island (northern Baffin Island area) counted 6,145 narwhals moving along the coast. From this, they estimated that there must have been 8,000 to 10,000 narwhals. For the most part, groups of males headed the migration. Mixed groups and young animals were most frequent in mid-July, and females with newborn calves occurred at the end of the migration. The peak of migration was 15 July when 1,842 narwhals were seen at a rate of 275 per hour between midnight and five in the morning. The usual group size was 3 to 8, but other groups were as large as 12 to 21.

Rolph Davis and his colleagues in an environmental research firm in Toronto, Ontario, have estimated that only forty percent of the Baffin Bay narwhals move along Bylot Island and that thirty percent pass along the Devon Island coast, and the other thirty percent move in mid-Lancaster Sound. From this they conclude that there must be at least twenty thousand and perhaps as many as thirty thousand animals in this northern population. This is up to two or three times the ten thousand estimated previously by Arthur Mansfield for Canada and northwestern Greenland." (HALEY, 1978).

The research programme begun by the biologists from Winnipeg included observation flights. So far, these have been restricted to the summer season, but it is essential that they be complemented by winter flights.

c. Feeding

The narwhal is essentially a squid-eater (TOMILIN, 1967). MANBY (1823), who accompanied the whaler "Baffin", commanded by Capt. Scoresby, Jr., to Greenland, writes (p. 66): "On 25 May 1821 a narwhal was harpooned. The narwhal's food consists of cuttle fish, of which I removed many from his stomach". This observation was confirmed by a second catch, on 25 July, near East Greenland at 74 30'N 12 W (p. 153): "During the butchering of this narwals I collected from his stomach pieces of his principal diet, namely crabs and sepia or cuttle fish. I obtained several excellent, previously described specimens of the latter". Scoresby (1820) found cephalopods (*Rossia*) in the stomach, and in one specimen, in addition to a flounder, a still undigested ray (*Raja batis*) measuring 70 cm in body length, and 51 cm in width. The author asks himself how the narwhal could swallow such a large fish without first killing it, and suggests that the narwhal killed the ray with its tusk.

MELDGAARD and KAPEL (1981) analyzed the stomach contents of an adult, male narwhal with a body length of 530 cm and found: 63 otoliths of the polar cod (Boreogadus saida), two cephalopod beaks (Gonatus fabricii), as well as crustaceans which probably came out of the fish stomachs. 24

I should like to add, concerning the behavior of the prey, that Rossia is a strictly benthic, bottom-dwelling genus among the cephalopods. The calmar Gonatus is constantly on the move. As neither is a luminescent cephalopod, one must assume that the narwhal locates them acoustically.

VAN BENEDEN (1889) reports the presence of cuttle fish in the stomachs of five narwhals. In addition, various authors found: Greenland halibut (Reinhardtius hypoglossoides), arctic cod (Boreogadus saida), sea scorpion (Acanthocottus), salmon, herring, and decapod crustaceans (BEDDARD, 1900; WINGE, 1902; SMIRNOV, 1935; DEGERBØL and FREUCHEN, 1935; CHAPSKII, 1941; VIBE, 1950; PALMER, 1956). According to TOMILIN (loc. cit.), fish and crustaceans are of secondary importance, and the pelagic food consists of cuttle fish (see also BROWN, 1868; GRAY, 1889). Unfortunately, there are no systematic investigations extant and, inasmuch as the narwahl is a migrating animal, its dietary habits vary according to its seasonal habitat. However that may be, what seems important to me is that a male narwhal, in spite of its fully developed tusk, can catch -- in addition to pelagic cephalopods, which he hunts in deep water -- ground fishes such as, for instance, the halibut.

In capturing the latter, the narwhal is said to use its tusk (DEGERBØL and FREUCHEN, loc. cit.), but the authors do not say how the animal might do this.

According the HELEN SILVERMAN (1979), the main food of the narwhals in the Baffin and Bylot waters is the arctic cod (Boreogadus saida), which lives close to the pack ice. She found remnants of these fish in the stomachs of 83.6% of the 73 narwhals she examined.

Pelagic fish sometimes hunt in formation. DEGERBØL and FREUCHEN (loc. cit.), in the Baffin waters, watched nine narwhals perfectly lined up side-by-side in a straight line hunting tom-cod (Microgadus). The stomachs of whales caught were filled to bursting with these fish. On the 12th of June (Eclipse Sound) they again saw narwhals: "but they were moving in rows of five to ten, not in a single file. In this manner they chase the small fish found in these waters ... an immense number of tom-cod no larger than a man's middle finger. The stomachs of the narwhals are now quite full of them". On the 14th of July, another narwhal was caught "with the stomach so stuffed with small tom-cod that it could hold no more. Nevertheless mouth, throat and even the corners of the jaws were stuffed; I have never seen an animal so replete".

According to DEGERBØL and FREUCHEN narwhals, in the fall, also catch salmon trout.

d. Palaeontology

We know extremely little about the phylogeny of the narwhal. KELLOG (1928) lists it in his geological and geographical table of the distribution of whales from the Sicilian (upper Pliocene) of Europe and the Quaternary of North America, without, however, commenting on these finds in his text. SIMPSON (1945) advances the same opinion in his "Classification". The reader will be surprised that KELLOG, in his work, includes the genus Monodon in the family Delphinidae! 25

Finds of fossil narwhals are extremely rare, and were made mostly at a time when the location of the site and its geological stratum were not considered to be of major importance. As BRANDT (1873) mentions, a tusk was found in the delta of the Lena river as early as the beginning of the last century; others in the river Aitscha in Eastern Siberia, on the Chatanga, Anabar, Olonek and lower Indigirka (Simowie), some of which were given to the Leningrad Museum. Most of these tusks are probably not very old; the last one, according to BRANDT, could date from the time when the Northern Ice Ocean extended to the middle of Siberia. Whether the tusk fragment described by OWEN (1846) comes form the London Clay (= Eocene), is difficult to ascertain.

Other finds, such as those from the coasts of Essex, from Lewes, are of uncertain date, as is the poorly preserved tooth from Falun de Sort, which VAN BENEDEN and GERVAIS thought might be a narwhal or sperm whale tooth.

COLLINGS (1933) described narwhal teeth from the early Pleistocene. Finds at Chaleur Bay, Gulf of St. Lawrence (late Wisconsin period) are early post-glacial, and demonstrate that in earlier times the distribution of the narwhal extended further south than today.

Besides the fossil teeth just mentioned, only very occasional remnants of skulls have been found. Because of this situation, the early history and original distribution of this recent species remain obscure and can hardly be followed even in the Pliocene.

FRANZ (1924) has the following to say: "However, not only the river dolphins, but also the short-beaked, white whale-like species of the Delphinapteridae, Delphinapterus (white whale) and Monodon (narwhal), unknown as fossils, with less numerous and usually weak teeth, should be considered , according to Abel, as the last offshoot of the sharp-toothed whales (Acrodelphidae) because certain skeletal characteristics seem to connect the latter to the former. It is not surprising that a species as uniquely differentiated as the narwhal, or "unicorn whale", should be short-lived in an evolutionary sense and therefore, because it lives today, would not be encountered as a fossil".

If this should prove to be correct, we may assume that narwhal evolution (= speciation) was rapid.

e. Some Special Morphological Characteristics

1. Skin (Common Integument)

The skin of *Monodon monoceros* (Pl. 5) has an unusual 26 pigmentation, the significance of which is unknown. The white whale, a species that is taxonomically close to the narwhal and shares its ecological niche, is entirely white. The color pattern changes with age. Foetuses at term and young animals are evenly dark grey to blue-black. As the animals become older, white areas develop, first around the anus and genitalia, then covering the whole ventral surface and extending onto the flanks and back. Adult narwhals are yellowish ventrally, and spotted with grey to brown-black dorsally (Pl. 4). However, the dark pigmentation gradually fades so that males in advanced age appear white. From this, KUKENTHAL (1899) concludes that phylogenetically the white whale (*Delphinapterus leucas*), for example, evolved from more darkly pigmented whales and did not acquire the white skin color until relatively late. The adult is hairless, but seven pairs of hairs have been demonstrated on the lower jaw of very young whale foetuses (EALES, 1950). Whether the follicles of these hairs persist in the adult is not known.

So far, we have no exact studies of the narwhal's skin, its topographical variations, or its histologic and histochemical characteristics, nerve receptors, and metabolism.

A regional study of the papillae which cover the entire body could be highly informative. This method was used by PURVES

(1963) in Delphinus and Phocoena in order to elucidate the mechanics of flow at high speeds.

As I suspect that the narwhal has a specialized manner of swimming (see Chapter on the fluke), analysis of the directional arrangement of the skin papillae could yield valuable results.

The skin of cetaceans consists, as that of terrestrial mammals, of an ectodermal epidermis with a subjacent corium (dermis), which, together with the subcutaneous connective tissue (tela subcutanea), make up the mesodermal layer of the skin. Beneath the tela subcutanea may be either adipose tissue (panniculus adiposus), muscle fascia or other structures.

JAPHA (1907), who studied the skin of the balaenopteridae divides the epidermis into a thin, outer stratum corneum and a broad stratum germinativum, which extends basally to the dermal papillae and the ridges of the corium.

In Monodon, where so far only one antero-lateral piece of the melon has been examined, the layers of the skin are sharply demarkated from one another by their pigmentation (Pl. 5). Even to the naked eye, two layers are evident in the epidermis, an outer, grey-reddish one, 0.8 to 1.0 mm thick, followed by a deeper, grey layer, some 2.0 mm thick. The connecting corium has an upper, light-grey layer 2.0 to 2.5 mm thick, with papillae disposed vertically to the skin surface, and a lower 2.0 to 2.5 mm thick, black basal layer attached to the subcutaneous connective tissue. Together, epidermis and corium measure 9 mm in thickness. By contrast, the thickness of these layers over the melon of Delphinapterus leucas is only 3 mm (Pl. 5).

In both species, the subcutaneous connective tissue (hypodermis) lies under the corium. In the region of the panniculus adiposus it appears as a clearly distinct, thin, whitish layer. The panniculus adiposus is absent over the rostrum and the anterior melon, and in those areas the subcutaneous connective tissue is much thicker.

It is clear that even macroscopically one can see that in narwhal and beluga the skin displays species-specific characteristics of unknown significance, even though the two species are closely related taxonomically and ecologically.

The narwhal displays a major thickening of the papillary layer, and with it, an increased vascularization of the skin (Pl. 5). This layer becomes nearly as thick as the epidermis. Over the melon, in narwhal, the ratio is 4:3, in Beluga 1.5:3.

2. Nervous System

A macroscopic atlas of the brain of the narwhal is in preparation, but I should like to discuss here already some of the major findings.

The brain of the narwal is highly developed. When fresh, it weighs 2,605 g. This corresponds to a relative brain weight -- brain weight (= 1) : body weight (= approximately 1,500 kg in an adult male) -- of 1 : 576. About 35% of body weight is blubber. If one subtracts the weight of this fat, which is not related to brain size, from the total body weight the ratio becomes 1 : 403. If one then enters these values into the graph representing cephalization, which I calculated earlier, the level of narwhal coincides approximately with that of beluga, Delphinapterus leucas (brain weight = approximately 2,300g) (PILLERI and GIHR, 1981) (Fig. 5).

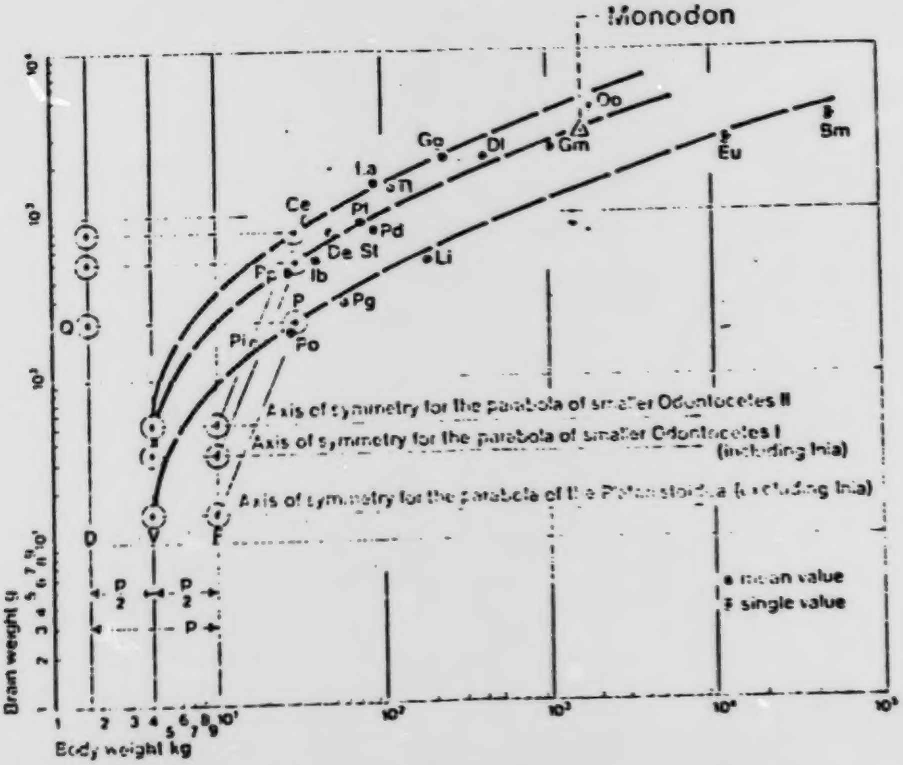

Fig. 5 Logarithmic graph giving brain weight as a function of body weight in cetaceans. Position of Monodon is indicated.

Bm = Balaenoptera musculus. Ce = Cephalorhynchus commersoni. De = Delphinus delphis. St = Stenella coeruleoalba. Dl = Delphinapterus leucas. Eu = Eubalaena australis, Gg = Grampus griseus. Ib = Inia boliviensis. La = Lagenorhynchus obliquidens. Li = Lipotes vexillifer, Oo = Orcinus orca. Pd = Phocoenoides dalli, Pg = Platanista indi, Po = Pontoporia blainvillei, Pp = Phocoena phocoena, Pt = Phocoenoides truei, Tt = Tursiops truncatus.

Monodon, therefore does not belong to the most cephalized Odontocetes. But its brain is highly differentiated, as shown by the strong corrugation of the cortex and the hypothalamic index (length of hypothalamus : length of cerebrum = 0.06). In *Delphinapterus leucas* I found an hypothalmic index of 0.06 - 0.07 (PILLERI, 1963).

The narwhal brain (Pls. 6 to 9) displays all the characteristics typical of the cetacean brain, with frontal lobes extending far basally, and main gyres arranged concentrically and rostro-caudally around the sulcus. The cerebellum is relatively well covered by the cerebral hemispheres. As in all the other whales, the brain is anosmatic and has eleven cranial nerves (Fig. 6). The one with the greatest diameter, 9 mm, is the vestibulocochlear nerve.

It is interesting that in the narwhal there has been a relative reduction in the calibres of the optic and the three occulomotor nerves, when one compares their respective diameters with those in *Delphinus delphis* (PILLERI *et al.*,1980). This reduction affects mainly the trochlear nerve (Table II) and probably correlates with the eye's lateral position (Fig. 7), which makes binocular vision impossible in

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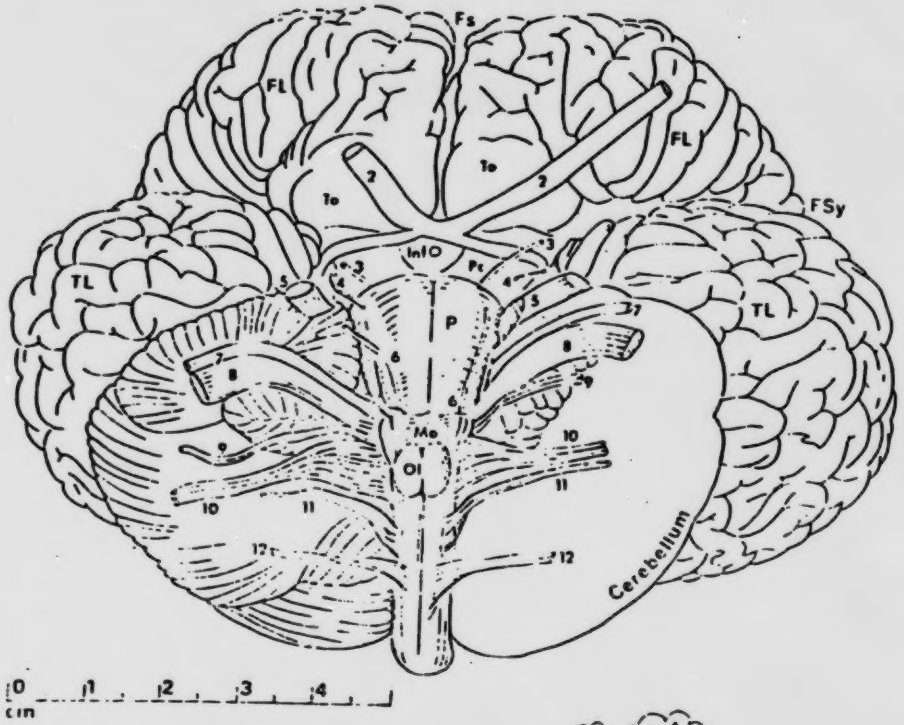
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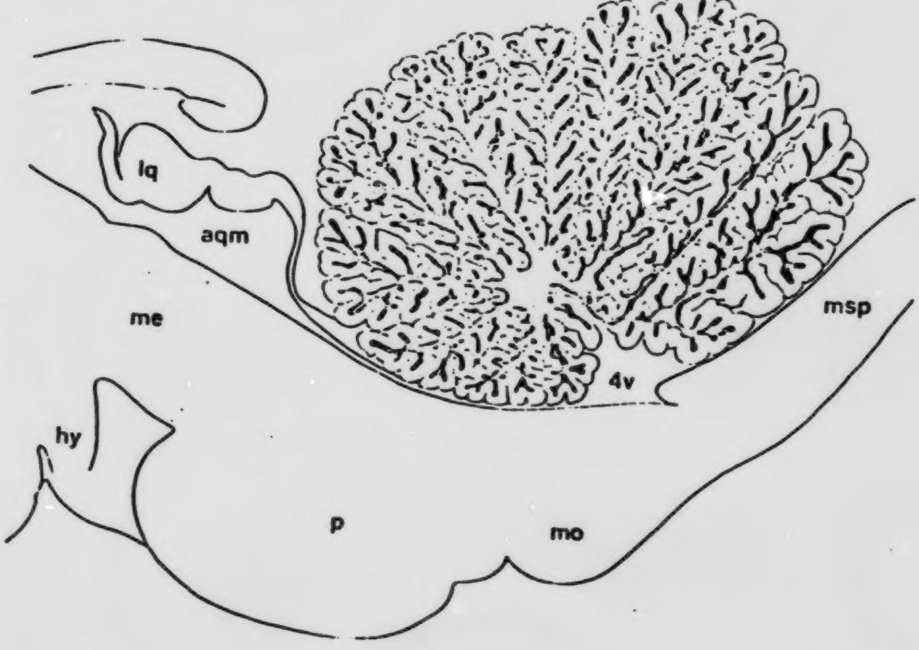
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Fig. 6 (A) Base of narwhal's brain, with cranial nerves.

FL = frontal lobe
FS = sagittal (longitudinal) cerebral fissure
FSY = Sylvius' fissure
Inf = infundibulum
Mo = medulla oblongata
O1 = inferior olive
Pc = cerebral peduncle
TL = temporal lobe
To = olfactory bulb
2 = optic nerve
3 = oculomotor nerve
4 = trochlear nerve
5 = trigeminal nerve
6 = abducent nerve
7 = facial nerve
8 = vestibulocochlear nerve
9 = glossopharyngeal nerve
10 = vagus nerve
11 = accessory nerve
12 = hypoglossal nerve

(B) Median-sagittal section through the vermis of the cerebellum.

aqm = mesencephalic [mid-brain] aqueduct
hy = hypothalamus
lq = lamina quadrigemina
me = mesencephalon
mo = medulla oblongata
msp = spinal medulla [rostral spinal chord]

the narwhal. When the eyes are positioned in this way, the function of the IVth cranial nerve -- which causes the superior 28 oblique muscle to rotate the eye down and outward (in the whale = caudad) -- is much reduced. Thus, function of the abducens nerve, which abducts the eye, i.e. turns it caudad in the whale, becomes the more important.

Much can be learned by comparing the narwahl's optic and oculomotor nerves to those of the beluga. In the latter species: the optic nerve is slightly narrower; the oculomotor and abducens nerves are about the same; the trochlear nerve is at least 3 X thicker than in Monodon. Beluga's binocular field of vision is directed rostro-ventrally, in much the same way as the sonar field (see PILLERI, 1982).

TABLE I 30,31.32

Brain Dimensions (in mm) of (a) Monodon monoceros and (b) Delphinapterus leucas.

A Animal number, sex
1 Overall length of brain
2 Length of cerebrum
3 Width of cerebrum
4 Height of cerebrum
5 Temporal lobe pole to caudal lobe pole
6 Temporal lobe pole to frontal lobe pole
7 Length of fissure of Sylvius
8 Smallest distance between temporal lobes

9 Width of olfactory bulb

10 Length of olfactory bulb

11 Length of cerebellar hemispheres

12 Height of cerebellar hemispheres

13 Width of cerebellum

14 Length of cerebellar vermis

15 Height of cerebellar vermis

16 Pons to apex of cerebellum

17 Width of midbrain

18 Width of lamina quadrigemina

19 Length (median) of lamina quadrigemina

20 Length of anterior (superior) colliculi

21 Width of anterior (superior) colliculi

22 Width of posterior (inferior) colliculi

23 Length of pons

24 Width of pons

25 Length of hypothalamus

26 Length of anterior pituitary

27 Height of anterior pituitary

28 Width of anterior pituitary

29 Neurohypophysis (longitudinal ø)

30 Height of neurohypophysis

31 Neurophypophysis (transverse ø)

32 Length of corpus callosum

33 Thickness (maximal) of corpus callosum

34 Genu of corpus callosum to frontal lobe pole

35 Mid-corpus callosum to border of longitudinal fissure

36 Width of medulla oblongata

37 Length of medulla oblongata (from pons to root of 1st. spinal nerve

38 Inferior olive (horizontal ø)

39 Inferior olive (longitudinal ø)

40 Inferior olives (combined width)

41 Optic nerve ø

42 Optic tract (beyond chiasma) ø

43 Oculomotor nerve ø

44 Trochlear nerve ø

45 Abducens nerve ø

46 Trigeminal nerve ø

47 Facial nerve ø

48 Vestibulocochlear nerve ø

49 Glossopharyngeal nerve

50 Cervical medulla [rostral spinal chord] (transverse ø)

51 Cervical medulla [rostral spinal chord] (longitudinal [? dorso-ventral] ø)

		(a)	(b)
A	Tier Nr.. Geschlecht	812, ♂[1]	200. 201. 202 ♂♂[2]
1	Gesamtlänge des Gehirns	170	160 - 165
2	Länge des Grosshirns	145	140 - 150
3	Breite des Grosshirns	220	180 - 190
4	Höhe des Grosshirns	125	110 - 140
5	Temporalpol-Kaudalpol	100	105 - 120
6	Temporalpol-Frontalpol	65	55 - 60
7	Länge der Fissura Sylvii	52	48 - 50
8	Kleinste Entfernung zwischen den Temporallappen	55	50 - 58
9	Breite des Tuberculum olfactorium	33	32 - 34
10	Länge des Tuberculum olfactorium	26	25 - 26
11	Länge der Kleinhirnhemisphäre	94	65 - 72
12	Höhe der Kleinhirnhemisphäre	55	40 - 45
13	Kleinhirnbreite	142	120 - 180
14	Länge des Vermis cerebelli	60	49 - 58
15	Höhe des Vermis cerebelli	42	40 - 45
16	Brücke-Kleinhirnscheitel	93	75 - 85
17	Breite des Mittelhirns	55	–
18	Breite der Lamina quadrigemina		
19	Länge der Lamina quadrigemina (median)	23	23 - 26
20	Länge der Colliculi anteriores	–	8 - 10
21	Breite der Colliculi anteriores	–	13
22	Breite der Colliculi posteriores	–	23
23	Länge der Brücke	36	37 - 40
24	Breite der Brücke	42	40
25	Länge des Hypothalamus	11	11
26	Hypophysenlänge (Adenohypophyse)	15	–

27	Hypophysenhöhe (Adenohypophyse)	13	-
28	Hypophysenbreite (Adenohypophyse)	30	-
29	Neurohypophyse (Längsdurchmesser)	10	-
30	Neurohypophyse. Höhe	7	-
31	Neurohypophyse (Querdurchmesser)	15	-
32	Länge des Balkens	60	50 - 58
33	Dicke des Balkens (maximale)	9	4 - 5 (Mitte)
34	Balkenknie-Frontalpol	33	30
35	Balkenmitte-Mantelkante	50	40 - 50
36	Breite der Medulla oblongata	31	-
37	Länge der Medulla oblongata (= vom caudalen Brückenrand bis zur 1. Spinalnerven-Wurzel)	40	-
38	Oliva inferior (horizontaler Ø)	9	-
39	Oliva inferior (Längsdurchmesser)	17	-
40	Olivae inferiores (Gesamtbreite)	18	-
41	Nervus opticus Ø	6	5
42	Tractus opticus (nach dem Chiasma) Ø	3	-
43	Nervus oculomotorius Ø	1.4	1.3
44	Nervus trochlearis Ø	0.3	1
45	Nervus abducens Ø	1.2	1
46	Nervus trigeminus Ø	8	8
47	Nervus facialis Ø	3	2.9
48	Nervus stato-acusticus Ø	9	8
49	Nervus glossopharyngicus	2.5	-
50	Medulla cervicalis (Querdurchmesser)	11	-
51	Medulla cervicalis (Längsdurchmesser)	10	-

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[1] Pond Inlet, Baffin Land, G. Pilleri leg., 26.7. 1982.

[2] Nowaja Semlja, A.V. Yablokov leg., 1957.

The narwhal's trigeminal nerve is somewhat heavier than
that of the dolphin. Comparison with the beluga reveals no
siginificant differences of the facial and vestibulocochlear
nerves; but in the beluga, as opposed to the narwhal, the 30
trigeminal and acoustic nerves are of approximately the same
thickness (Table II).

The Pituitary

The anterior pituitary (Pl. 10) is bean-shaped and set transversely. It has two longitudinal, basal sulci. Next to it lies a much flattened, half-moon-shaped neurohypophysis. The infundibulum is 12 mm long. The pituitary is located outside the dura, embedded in a dense rete mirabile and enclosed in a capsule which arises from the dura and inserts fine septa between the anterior and posterior lobes of the pituitary. At their cut surfaces, both parts show similar consistencies, with grey-brown, marbled parenchymae; they can be distinguished from one another only through the presence of the dividing septum.

TABLE II

Comparisons of the diameters (in mm) of the Cranial Nerves of Monodon monoceros, Delphinapterus leucas and Delphinus delphi.

		A	B		A	B		A	B
Species	Monodon monoceros	in % des N.VIII	in % des N.II	Delphinapterus leucas	in % des N.VIII	in % des N.II	Delphinus delphis	in % des N.VIII	in % des N.II
N. opticus	6	67	100	5	62	100	5	77	100
N. oculomotorius	1.4	16	23	1.3	16	26	1.45	22	29
N. trochlearis	0.3	3	5	1.0	12	20	0.8	12	16
N. abducens	1.2	13	20	1.2	15	24	1.	15	20
N. trigeminus	8	89	-	8	100	-	4.5–5	69–76	-
N. facialis	3	33	-	2.9	36	-	3	46	-
1 . N. stato-acusticus	9	100	-	8	100	-	6.5	100	-

A = "as a percentage of the VIIIth cranial nerve"
B = "as a percentage of the IInd cranial nerve"
1.= vestibulocochlear nerve

3. EYE

Compared to the size of the animal, the eyes are relatively small. The horizontal diameter of the eyeball (3.4 cm) corresponds to 0.7% of body length (in beluga: 0.56%). The eye is positioned laterally and relatively high on the head, about midway between the dorsal and ventral surfaces (Fig. 7). When eyes are in such an extreme, lateral position -- similar to those in the sperm whale or in Platanista -- the visual fields must be oriented primarily toward the sides, which suggests that binocular vision is impossible. In beluga, where the eyes are directed antero-ventrad, the situation is entirely different (Fig. 7.).

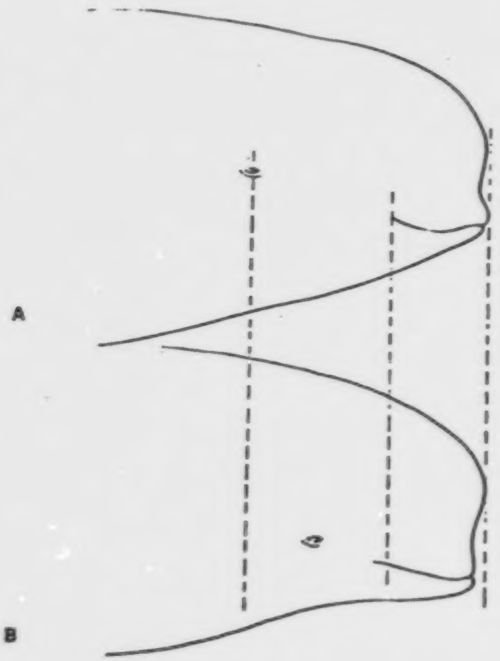

Fig. 7 Lateral position of eye in (A) narwhal, compared to (B) Delphinapterus leucas. Redrawn from photographs.

Beluga, when it is "standing" with its head out of water, can see in the ventrad direction; in its normal swimming position, it looks down (see Figure in PILLERI, 1982).

Macroscopically, the eye of the narwhal has all the typical cetacean characteristics (Pl. 11). The horizontal diamater of the eyeball is greater than the vertical one, and axially, the bulbus is much narrowed. The cornea is relatively thin, while the sclera, as in other species, is much thickened especiallly in the vicinity of the optic nerve. The slightly oval pupil does not have an operculum. The lens is spheroidal. 35

Immediately behind the eyeball, the ocular nerve is surrounded with an extensive *rete mirabile*. I expect additional details to come from the histological examination of the collected materials. The dimensions of the eye structures are listed in Table III. Compared to the eyeball of *Delphinapterus leucas*[*] (PILLERI, 1964), that of beluga is approximately 1/4 smaller (Table III).

Even though there are, at present, neither microscopical nor physiological observations of the narhwal's eye, there are indications that the animal has excellent

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(*) Translator's Note: Misprint for *Monodon monoceros*

		(a)	(b)	(b) in % of (a)
1.	Horizontaler Durchmesser des Bulbus	34 mm	25 mm	73.5%
2	Vertikaler Durchmesser der Bulbus	32 mm	23 mm	72 %
3	Länge des Bulbus oculi	24 mm	19 mm	79 %
4	Cornea, horizontaler Durchmesser	21 mm	16 mm	76 %
5	Cornea, vertikaler Durchmesser	20 mm	13 mm	
6	Cornea, Dicke	1 mm	1.4 mm	
7	Pupille, horizontaler Durchmesser	9 mm	–	
8	Pupille, vertikaler Durchmesser	7 mm	–	
9	Sklera, Dicke aequatorial	2 mm	1.7 mm	
10	Sklera, Dicke nahe Opticus	5 mm		
11	Nervus opticus, Durchmesser (im Rete-bereich)	4 mm	3 mm	
12	Rete mirabile, Durchmesser um den N. opticus	15 mm		

Table III. Comparison of eye measurements between (a) Monodon monoceros, male and (b) Delphinapterus leucas

1. Horizontal diameter of eyeball
2. Vertical diameter of eyeball
3. Length of eyeball
4. Cornea, horizontal diameter
5. Cornea, vertical diameter
6. Cornea, thickness
7. Pupil, horizontal diameter
8. Pupil, vertical diameter
9. Sclera, thickness at equator
10. Sclera, thickness near optic nerve
11. Optic nerve, diameter (in region of rete)
12. Rete mirabile, diameter around optic nerve

vision. This opinion is supported mainly by the nature of the seas in which it lives: subpolar water is very clear, and on sunny summer days, depth of vision is considerable.

This is supported by one of MANBY's (1823) observations. His ship, the "Baffin", was cruising in the waters of East Greenland, at a latitute of 74° 30'N and a longitude of 12° W: "If the ship had not been surrounded by ice, one would never have thought that we were in the arctic regions; never did the sun shine so brightly in England, and under the influence of all this light, the thermometer read 66°. 36

The warmth of the sun stimulated the creatures of this cold sea. From all sides one could hear the loud blowing of the unicorns [= narwhals], the males were chasing the females, and everything was in an unusual state of euphoria. The ocean was so astonishingly transparent that I could clearly recognize a narwhal (sea-unicorn) at least one hundred feet down. Not only did I see it clearly turning on its side to look at the boat, but I also distinctly recognized that it was a female". ...

Disregarding for the moment the histological details, which I hope to consider later, it seems to me that the extreme lateral position of the eye is a feature of major interest.

4. Hearing Organs

So far, there has not been any in-depth examination of the organ of hearing of Monodon monoceros. After DORAN (1876) described the auditory ossicles of the narwhal, KELLOG (1928) published a much simplified diagram of the bony parts of the ear without textual comments. ERNST HUBER (1934) produced drawings of the external auditory canal which were published posthumously by KELLOG and which, in spite of being incomplete, provide valuable information. KASUYA (1973) examined the tympanum and the periotic structures only from the point of view of their comparative osteological and taxonomic relationships, without studying in detail the structures of the middle and inner ear. NELLIE B. EALES (1951), using the wax-plate method, made a reconstruction of the ossicles and labyrinth of a narwhal foetus with a body length of 150 mm.

I am planning to use my material to complete our knowledge of the inner ear, in particular by a study of its histology. Until such time as it is completed, I should like to present some preliminary ideas concerning theories of audition in the cetaceans.

Theories about sound production in whales are full of mistaken views; so too, is the literature concerning sound (= echo) perception, which is replete with erroneous ideas harking back, in part, to KELLOG (loc. cit). These are held in particular by those American workers who deny that the external and middle ear have an auditory function.

In this view, the external auditory meatus, the tympanic membrane and the chain of middle-ear ossicles are all "vestigial", rudimentary, and thus "non functional". Sound or echos are said to be perceived by the lower jaw through "acoustic acids", then transmitted via the maxillomandibular articulation by pure bone conduction to the cochlea. In opposition to this theory, which is still today enjoying world-wide credibility, PURVES and PILLERI (1983) argue that whales and dolphins hear in just the same way as terrestrial mammals, 37 and that the structural modifications of the external and middle ear are merely expressions of an adaptation to life in the water and to pressure relations during diving.

The idea that the middle ear is fully functional gains further credibility when one considers the structure of the external auditory meatus. The drawings of HUBER (1934) show how well-developed the narwhal's external auditory meatus and its musculature actually are. From a tiny outer ear opening there extends a powerful, twisting meatus, actuated by fully developed muscles. The external auditory meatus consists of two parts, one proximal and cartilaginous, the other distal and membranous. The proximal part has a loop which holds an oval fat body of unknown function and homology (Fig. 8).

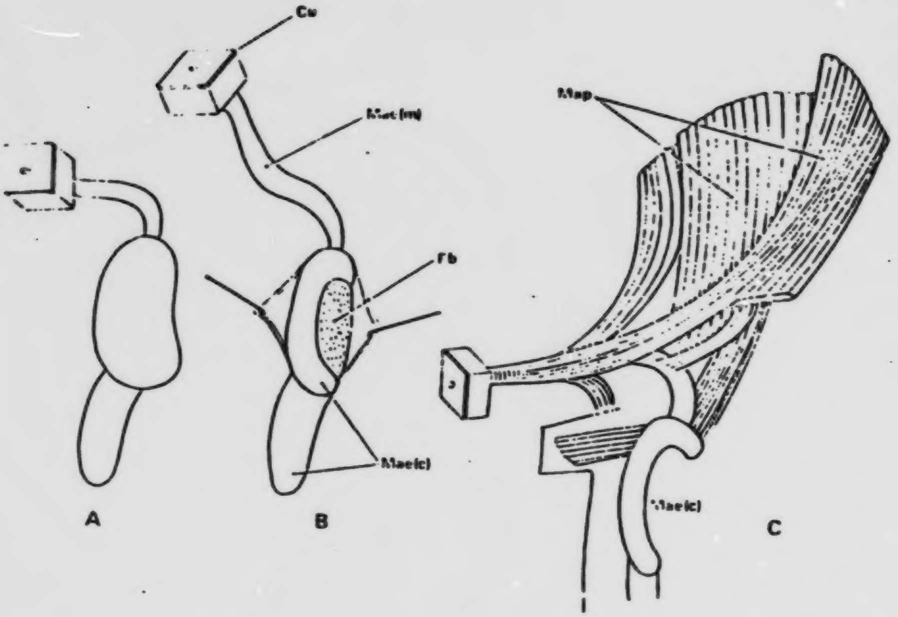

Fig. 8 External auditory meatus of narwhal. (Redrawn from HUBER, 1934)

Cu = skin
Fb = fat body in meatal loop
Mae(c) = cartilaginous portion of meatus
Mae(m) = membranous portion of meatus
Map = posterior auricular muscle

The meatal musculature is remarkable and consists of several muscles that attach even to the membranous portion, nearly as far as the outer opening of the auditory meatus. There can be no doubt that these muscles have remained functional, and that their actions affect the position of the meatus within the panniculus adiposus and the width of the meatus itself.

HUBER (loc. cit.) himself has left in his notes the following sentence: "Through joint action of these slips, the collapsed part of the lumen could be dilated".

Considering these findings, there can be no question of a degeneration of the external acoustic meatus in the narwhal. A similar situation could be shown to exist in the auditory meatus of the Indus dolphin, Platanista indi (PURVES and PILLERI, 1972), and other species. Our next task will be to identify more specifically, and to find the homologies of, the meatal muscles of the narwhal. 38

In HUBER's diagrams, these muscles are shown dissected and isolated, not in situ. It is therefore difficult to compare them with the muscles of other species, such as, for example, Delphinus delphis (Fig. 9). In view of their size in

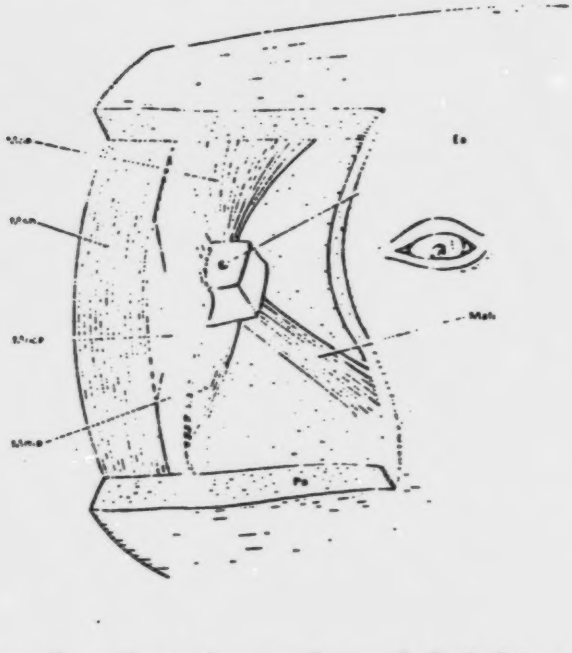

Fig. 9 Meatal muscles of Delphinus delphis.
E = eye
Ea = external opening of auditory
(names of muscles do not require translation)

the narwhal and the specificity of the anatomical preparations, one may assume that these are the same muscular organs as in the other cetaceans.

The narwhal's tympanic membrane is well developed and resemble that of the other odontocetes. The tympano-periotic structures (Pls. 12, 13) are also well developed and have the following dimensions:

1. Bulla. Länge	47 mm
2. Perioticum. Länge	54 mm
3. Distanz zwischen Processus sigmoideus und Aussenrand der Bulla	36 mm
4. Processus sigmoideus. Länge	17 mm
5. Processus sigmoideus. Breite	6 mm
6. Petrosum. Länge	23 mm
7. Innere Gehöröffnung	8 × 5 mm

Table IV.

1. Length of tympanic bulla
2. Length of perioticum
3. Distance from sigmoid process to external wall of bulla
4. Length of sigmoid process
5. Width of sigmoid process
6. Length of petrous region
7. Internal auditory meatus

A clear-cut, progressive development can be seen also in the ossicles of the middle ear (Pls. 14, 15, 16), as shown by a comparison of their weights (in grams) with hose of human ossicles. 39

Tabelle V

Species	Monodon monoceros		Homo sapiens (nach VIERORDT, 1906)	
Malleus	0.07		0.023	
Incus	0.25	Total: 0.33	0.025	Total: 0.050
Stapes	0.01		0.002	

The table shows that in Monodon the malleus weighs 3 X, the incus 10 X, and the stapes 5 X more than the corresponding ossicles in the human. Their total weight, in Monodon, is 6.06 X that in humans. Similar weighings, by BOENNINGHAUS (1903), showed that the ossicles of the porpoise, Phocoena phocoena, were five times heavier than those of humans, and three times heavier than those of the horse.

I find the extraordinary development of the incus in the narwhal quite remarkable; it occupies a major portion of the tympanic cavity. In some (young) animals one can remove the stapes quite easily from the oval window by means of a 40 forceps, in others it falls off by itself during maceration. In still others, the stapes is more strongly anchored in the oval window, suggesting that in these cases there may be ankylosis with the petrous bone (Pl. 16). There has been much discussion of this ankylosis in the older literature, and even today, authors are not in agreement on the physiologic significance of stapedial ankylosis, which was described for the first time by HYRTL (1845). Contemporary authors denied, because of this ankylosis, that the stapes had any possibility of movement, and concluded therefrom that any role in mechanical transmission of sound would be impossible. BOENNINGHAUS (loc. cit.), who discovered stapes ankylosis in Phocoena phocoena (5 specimens), suspected, in this species, a "molecular" form of sound transmissions.

I think that stapedial ankylosis is not, in any way, an obstacle to sound transmission. Whales and dolphins orient themselves by means of ultrasound and can hear echos of extremely high frequencies. With such high frequencies (200 kHz and higher), the stapes should be capable without trouble to transmit sounds from the tympanic membrane to the inner ear.

As I see it, the stapedial ankylosis maximally tightens the articulations, and is therefore an indication that the animals can hear supersonic sounds.

In the narwhal, the tight junction between the tympanic membrane and the incus by means of the short process should be considered from the point of view of orientation by ultrasound. One can not expect to observe in cetaceans vibrations of these structures, as one can in terrestrial mammals. One must remember that in the human ear even loud noise produces only microscopic displacements of the tympanic membrane. In the case of a high-frequency tone, the excursion of the vibrating membrane may be no more than one tenth the diameter of a water molecule!

I can summarize these preliminary findings as follows: in the narwhal, contrary to KELLOG's (loc. cit.) assumption, the external auditory meatus as well as all the structures of the middle ear are fully functinal in every way. Ankylosis of the stapes is relevant to the transmission of vibrations of ultra-high frequency to the cochlea. As in other cetaceans, the path that sound follows is: external auditory meatus, tympanic membrane, Folius' process [*processus anterior mallei*], head of malleus, body of incus, long process of incus, stapes, labyrinth.

5. The Tusk

The narwhal's most distinguishing, and still most puzzling
characteristic is doubtless the long tusk (Table 8). In the
15th and 16th centuries the tusk, thought to be the best
universal remedy, was worth ten times its weight in gold. A
narwhal tusk was one of the most guarded relics of the church
of St. Denis in Paris; another was in San Marco's basilica in
Venice. A tusk was also, next to the famed Farnese cap, the
pride of the Medici collection in Florence. Queen Elizabeth I 41
owned, and kept at Windsor Castle a tusk which was then valued
at 100,000 pounds. A magical representation of its curative

powers made that tusk one of the most coveted rarities of its times. The demystification of narwhal tusks began when Ambroise Paré (1510-1590) -- together with Lister and John Hunter one of the three greatest surgeons of all time -- managed to poison pigeons, to which he had fed powdered narwhal tusk, with arsenic: the tusk-nostrum could not prevent the arsenic's lethal effects.

Finally there appeared the description of the narwhal skull by OLE WORM (1638), a Danish naturalist. The study had been stimulated -- paradoxically, because Denmark, with the other Skandinavian countries, was exporting narwhal tusks -- by some Copenhagen merchants.

To WORM belongs the honor to have been the first to show that the fabled unicorn of the Middle Ages was a cetacean, which he named Unicornu marinum (Fig. 10).

The tusk described by WORM is broken off distally (loc. cit. p. 285: "dens ipse integer non erat, sed tertia ferme sui partis mutilus, quinque interim pedes longus"...[the tooth was not whole, but a full third of it mutilated, the rest, five feet in length"...]).

I find the distal abrasion which developed in situ (WORM, loc. cit. Fig. on p. 283) on the left side of the tusk, particularly interesting.

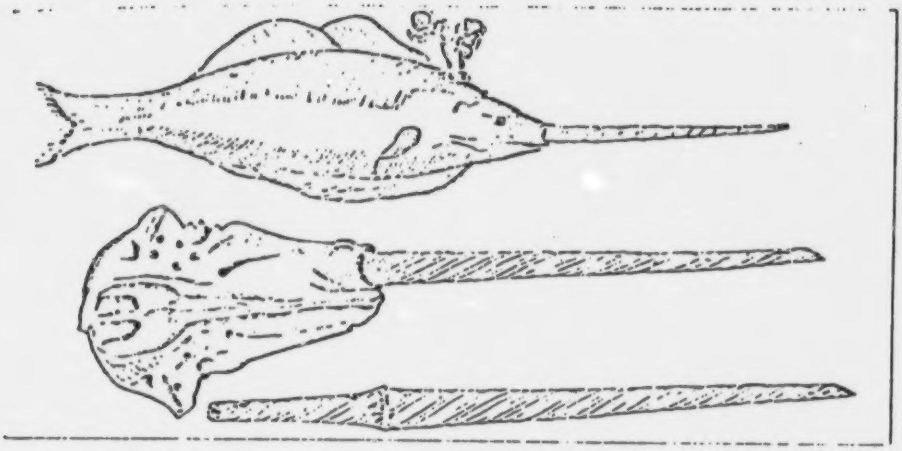

Fig. 10 Representation of Unicornu marinum by OLE WORM (1638)

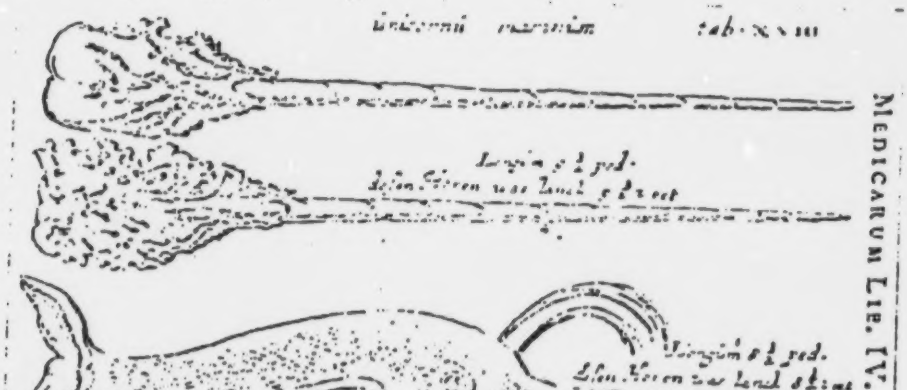

Fig. 11 The narwhal, after TULPIUS (1672)

In the subsequent period one finds further descriptions, such as those of a male narwhal stranded in 1648 in the British Isles, by the anatomist NICOLAUS TULP (TULPIUS) and published in "Observationes medicae (editio nova, 1972). TULP shows (Fig. 11) inverted cement spirals, but the animal's shape appears somewhat more natural than in WORM, 42 who drew two dorsal and one long ventral fins, in addition to a fish-like, vertically positioned tail. KLEIN (1741) was already more accurate, in spite of the bad proportions of the whale's body. The drawing made by PONTOPPIDAN (1755) is full of phantasy, but WILLUGHBY's (1685) representation, at least the picture of the isolated tusk with exact rendition of the spirals, is very true to nature.

In a few, rare instances, the tusk may reach a length of 3 meters and a diameter, at the neck, of 10 cm (TOMILIN, 1967). The specimen I collected at Pond Inlet has a total length of 2.33 m; the root is 38 cm long and the neck has a diameter of 6.2 cm (Pl. 17).

The tusk of the narwhal consists of an inner column of dentine, surrounded by a spirally wound layer of cement (Pl. 18; Fig. 12). There is no enamel. The pulp cavity is wide at the level of the root,then continues distally as a narrow channel in the crown and extends nearly to the tip. The pulp cavity does not have a uniform diameter, but is segmented by slight constrictions, clearly seen on X-rays, that

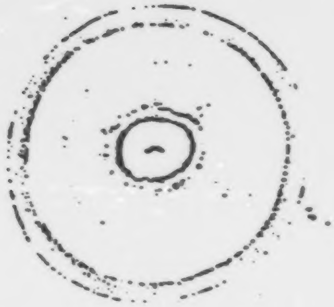

Fig. 12 Cross-section of narwhal tusk; after VAN BENEDEN and GERVAIS (1880)

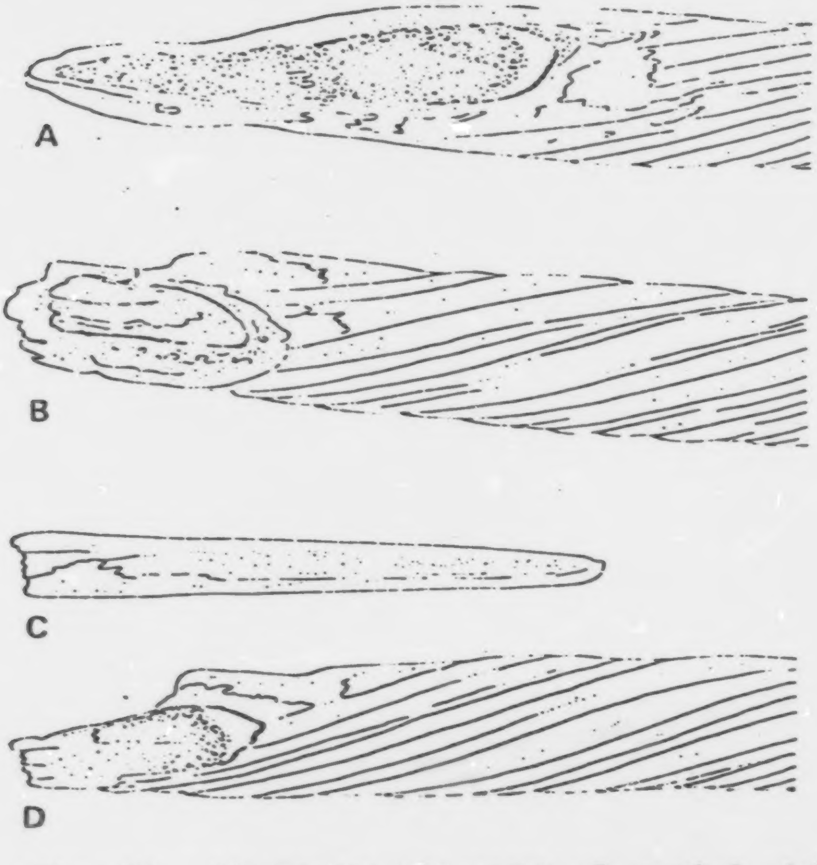

Fig. 13 (A) Broken-off tooth of narwhal with extensive abrasions. (B) Other specimen, with dentine cylinder in situ. (C) dentine cylinder alone. (D) Tooth after removal of cylinder.

reflect the spiralling pattern (Pl. 19). The spongy pulp bleeds copiously when the tusk is removed or broken, and may partly run out of the cavity. Broken teeth cicatricize by forming dentine in the pulp cavitiy. This produces a dentine cylinder which, in a dessicated tooth, can be removed from the pulp cavity (Fig. 13). DEGERBØL and FREUCHEN (loc. cit.) found remnants of mud and small stones in an open cavity of a broken tusk, proof that the narwhal roots at the bottom of the ocean even with a broken tooth. According to the work of DOW and HOLLENBERG (1977), the pulp does not "differ fundamentally from that of other mammals", except, I think, in so far as 44
vascularization is concerned.

The latter is rete-like in character, with thick-walled arteries. Because fat cells, with their "acoustic lipids", are absent, the authors exclude the tusk from any involvement with the sonar system. As I shall explain later, this assumption is misleading. Unfortunately, so far most significance has been attributed to the tusk's external shape. There are no studies extant -- histologic, biochemical or physical/acoustic -- concerning the tusks's hard components. The only existing study of the pulp shows that the pulp is a vital structure which is enabled, by its construction and vascularization, to withstand variations of pressure and temperature. It is interesting to note (DEGERBØL and FREUCHEN, 1935), in this connection, that teeth that have been removed, quickly lose up to 16% of their original volume and weight through dehydration. Rapid drying causes longitudinal longitudinal clefts that do not follow the spirals. 45

The tusk is sensitive to traumatization, and can break off. PORSILD (1922) could show that among 314 specimens found, no fewer than 107 (approximately 30%) had been broken off. PEDERSEN (1930) writes: "Damaged tusks, in which the tip had been broken off, were often found". Spontaneous fractures are always oriented either dorso-ventrally or ventro-dorsally, never horizontally (DEGERBØL and FREUCHEN, loc. cit.).

Though otherwise edentate, the narwhal develops an only tusk, which corresponds to a left maxillary incisor with a quadruple anlage (FRASER, 1938). Males nearly always have a tusk and are rarely edentate. PEDERSEN (1930) and HAY and SERGEANT (1976) observed, each, an adult male devoid of tusk. Females very rarely have a tusk, and those with two are rarer still. Immature animals of either sex have two, frequently four, undeveloped teeth (Fig. 14)[*]. Males with two tusk are encountered regularly, if not frequently (Figs. 15, 20), and in these the right tusk is usually the smaller one (CLARK, 1871). The spirals in the cement are directed toward the left and the tip. When two tusks develop, they spiral in the same direction (Fig. 15). SCORESBY's (1823) finding of a female with a left-

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(*) Translator's Note: In the original, this and the previous sentence have been garbled and intermingled. The reconstruction of the translation is reasonable, but not certain.

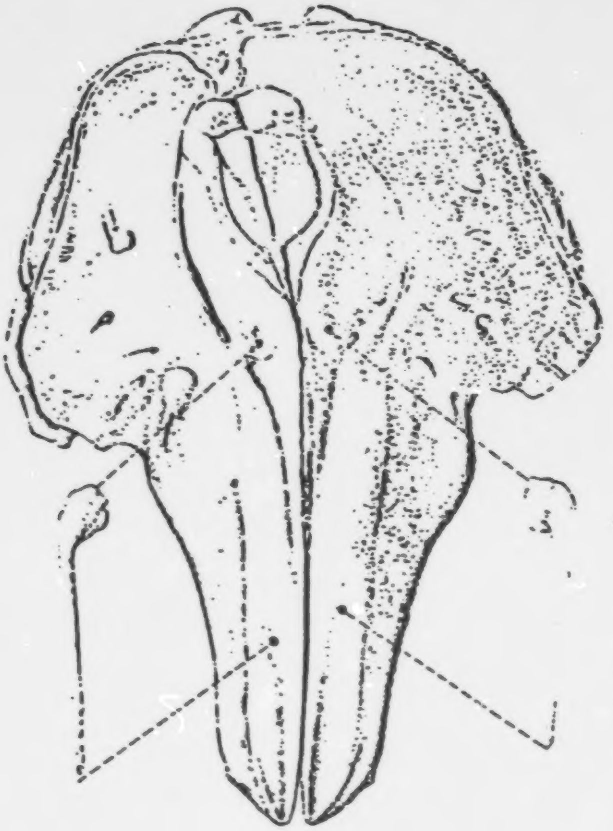

Fig. 14 Undeveloped tusks of female narwhal. After VAN BENEDEN and GERVAIS (1880)

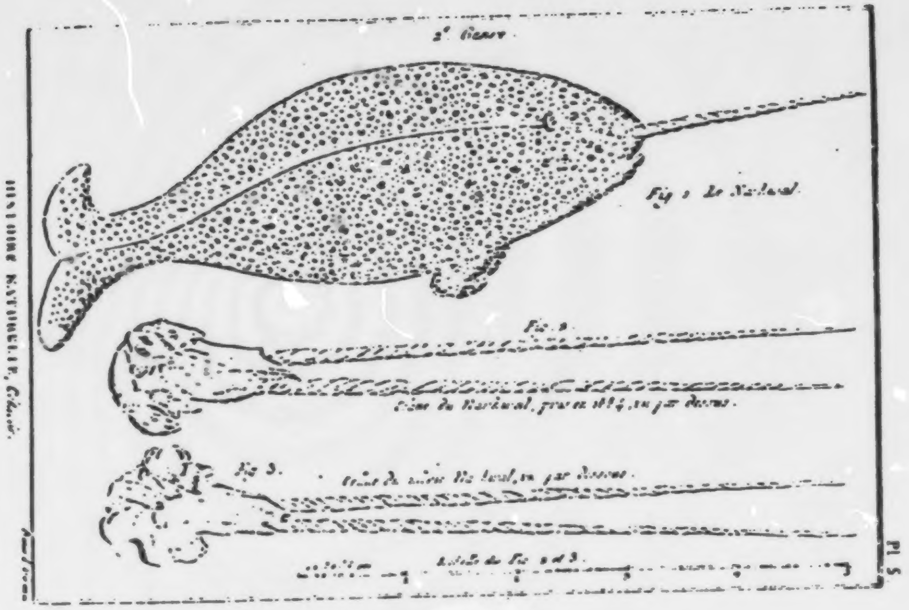

Fig. 15 Two-tusked, male narwhal, as shown on a drawing from the 18th Century. (From the collection of Dr. T. De Monte, Trieste).

sided, right-and-distad spiraling tusk is probably a unique observation. After the fact, it was impossible to confirm this discovery. Foetal teeth do not spiral (FRASER, 1938).

The spiraling stops several centimeters below the tip, which is always smooth, even if there are two tusks in the same animal. I should further like to draw attention 46
to the slanting abrasions on the tusks, which are also found in broken-off teeth when the fracture has been cicatricized for some time. During life, the tusk is covered by algae (*Rhodochorton*)(see Pl. 18). At the edge of the gingiva, near the neck, there is a small, collar-like population of whale-lice (*Cyamus nodosus*, *Cyamus monodontis*).

f. Function of the Tusk

The exact functional significance of the tusk so far still escapes cetologists. SCORESBY (1820) considered it to be a harpoon for spearing fish. BEDDARD (1900) thought that the tusk might be of use to the males in their rutting fights. WINGE (1921) saw it as a rake, used by the narwhal to obtain food from the sea bed. CHAPSKII (1941) considered it exclusively as a characteristic of sexual dimorphism, even though this is not 100% accurate. In the most widespread view, the tusk is used in winter to break open breathing holes in the ice (TOMILIN, 1967). This would be consonant with PORSILD's (loc. cit.) discovery of many broken teeth. Yet PORSILD himself is of the opinion that narwhals use only the melon to break open the ice cover (as killer wales are known to do). TOMILIN further thinks that the whale uses the tusk to defend juveniles and females against the attacks of the Greenland shark (Somniosus microcephalus) (SMIRNOV, 1941). Narwhals are also attacked by killer whales (Orcinus orca)(DEGERBØL and FREUCHEN, 1930; STELTNER, 1982). However, it could not be ascertained whether they defend themselves by means of the tusk. Just exactly how narwhals defend themselves against walrus, which also attack narwhals, has not yet been observed.

To summarize: so far, we lack concrete proofs concerning the real use of the tusk, particularly as our knowledge concerning the whale's behavior is extremely scant.

It seems to me that the tusk has several purposes and that its function may have slowly altered during the evolutionary history of the species. One must also assume that at the species'origin, the tusk was of much smaller dimensions. The fact that most females are tuskless seems to me not to have a real bearing on any possible explanation of the tusk's function.

Both in captivity (Vancouver aquarium) and in the wild, the male can be observed touching the female with his tusk. One most reliable observation, made in the field, 47
stems from FRIDTJOF NANSEN (1898; Vol. II; pp. 401-402): "A few days later we again were paid a visit by a troup of these

actors, in an other crevasse, which had newly formed quite close to the ship. Three of them had long, heavy tusks, which they sometimes held high above the water, sometimes used to scratch the backs of their girl friends".

This observation proves that the tusk has a tactile function, in addition to others. It has also been mentioned that when they sleep, they lay the tusk on the edge of the pack-ice, and rest for a while in this position, with the melon out of the water. In a narwhal harpooned by the "Baffin" in 1821, the tip and the entire underside of the tusk were polished and free of algae, which covered only the upper part (SCORESBY, 1820). In my opinion, the algae-free area was produced most probably when the animal rubbed the tusk against the edges of ice floes. Fights between narwhal bulls have never been observed, and all the Inuit I questioned confirmed that narwhals are extremely peacful, sociable animals, which never -- even in the panic-inducing situation of a "savssat" -- wound one another.

g. Morphogenesis of the Tusk

There can be no doubt that the tusk represents an overspecialization in this species, which may be analogous to the long tusks developed by some mammoth species.

In addition to quesions concerning its function, there is also the question concerning the tusk's genesis, and in particular the genesis of the spirals in the cement covering its surface. This biologically important question has so far been asked only by D'ARCY THOMPSON (1966), though entirely on a theoretical level. In spite of the fact that no one took the trouble to verify his assumptiom, or to discuss it in the light of factual arguments, no one accepted it, either (see, among others, REEVES and TRACEY, 1980).

For me, in view of my ontogenic observations on the fluke of the narwhal, D'ARCY THOMPSON's theory has regained significance. A towering authority in the field of "Growth and Form", THOMPSON devotes an entire chapter to the tusk of the narwhal, a chapter from which I shall quote verbatim:

"The "Horn" **of the Narwhal**

The "horn" or tusk of the narwhal is a very remarkable and rather unusual structure. It is the only tooth in the skull of the animal that matures; it reaches the enormous length of 8 to 9 feet and looks hefty; it never bends nor curves, but always grows arrow-straight -- a most rare and unusual phenomenon. At first sight, it appears to be twisted; 48
but in reality its straight axis supports a screw with several consecutive, gently ascending spirals; finally the most remarkable feature remains to be mentioned: when, as sometimes happens, two tusks arise instead of a single one -- one tusk on each side -- then these two do not form a coordinate or symmetrical pair; they are not mutual mirror-images, but identical screws, the gyres of which run in the same direction.

As we have seen, all ordinary teeth are, each in its own and natural way, more or less curved, a characteristic that becomes more clearly and more remarkably noticeable, the longer they are. One can not assume that the (inner and outer) fields of force within which the tusk of the narwhal develops are so uniformly simple and homogeneous that the tusk can grow, year after year, in total symmetry, without the least diversion to one side or the other; we must assume, rather, that the resistances the growing tooth encounters even-out and cancel one another, so that there can be no favouring of one side over the other. It is generally considered that the long, straight, pointed tooth is characterized by a "spiral twist"; but there is absolutely no twisting involved; the ivory consists of straight fibers, and its composition is uniform throughout. In short, the tusk is a straight, left-turning, shallowly-wound screw or snail's shell spiral with several gyres; it is these gyres which, formed from alternating grooves and ridges, twine themselves regularly and continuously about the tooth, from one end to the other, and even extend onto the root which lies deep within the tooth socket, or maxillary alveolus.

How this composite spiral is formed is totally unknown. We have just seen that it is not caused, for instance, by a twisting of the dentine axis. The fact that its course is, from beginning to end, uniform and uninterrupted suggests that the tooth somehow forms it as a unit; its extension deep into the maxillary alveolus, clearly demonstrates that it is neither embossed on, nor engraved in the tooth by exogenous influence. We also noted that the various grooves and ridges which make up the composite structure display individual or chance differences; a broader or narrower groove thus extends unchanged and clearly recognizable from one end of the tooth to the other; in other words: so long as growth continues, that which causes the formation of the grooves and ridges, whatever it may be, always acts in the same direction. A screw is usually formed by a combination of a translational with a rotational movement; for this, the rotation is under constraint from a pattern or matrix by which the thread is then formed or defined; I can not avoid thinking that the tooth of the narwhal, during all of its growth, similarly and very slowly, rotates about its long axis - no matter how unique, unusual and difficult to imagine such a growth pattern may be. We know that the tusk grows in length throughout life, which may be attributed to the open root and "permanent pulp"; only simul- 49 taneous and continued turning explains (in my view): the absolute straightness of the tusk; the grooves -- the "rifling" -- that are formed on the surface in the absence of any twisting of the core on the inside; the extension of the rifling over the alveolar section of the tooth, inside the jawbone; the fact that grooves and ridges which are contiguous retain, severally, their own individual shapes as they grow and spiral along the tooth. The only requirement is a very slow rate of rotation, about four or five turns of the tooth during its entire life-time.

The progress of a whale or dolphin through the water can be represented as the reaction to a wave which moves from head to tail, and during the progress of which the animal moves slightly slower than the wave in the water. The same principle also applies to fish, but in the fish the waves are in a single plane, kept there with the assistance of the dorsal and ventral fins; but in dolphin they appear to be "circularly polarized": i.e. resoluble into two waves, moving in planes normal to each other and caused by the beating of fluke and peduncle in circular movements the phases of which change from one cross-section to the other. This wastes some energy, much as do a ships's screw and a torpedo (where it is specially corrected for and compensated); the wastage is caused by the presence of a "harmful moment" which tends to make the body rotate about its own axis so that the animal swims by "screwing" itself forward through the water. A slight left bend of the tail, in the dolphin, partially corrects for this tendency. Research done by W. Shuleikin on the dynamics of the dolphin -- a major experimental as well as theoretical investigation -- proves that the dolphin is a better swimmer than the fish in that the speed with which it moves forward more nearly approaches the velocity of the wave propagating along its body; the so-called "step", or fraction of body length travled during one wave phase, is approximately 0.7 in the dolphin and 0.57 in a rapidly swimming fish (tunny or mackerel).

Shuleikin makes the curious remark that the asymmetry of the skull (recognizable in some cetaceans), which in the dolphin has a screw-twist with a pitch about equal to the length of the body, has a retarding effect on the screw-type motion during forward progressions: this would explain the "so far unknown purpose of the skull's asymmetry[*] . I should say this in an other way by suggesting that the counter-spirality of the skull is the immediate *result* of the spiral component of forward motion. This implies, I belive, a retarded and incomplete response of the front part of the body to 50 the rotatory impulse of the rear end or, in the simple language of the engineer, *torque of inertia*.

This tendency, faintly indicated in the dolphin's skull, is clearly expressed in the "horn" of the narwhal, and provides a full explanation for its many characterisitcs. The narwhal and its horn are closely coupled, and move as a single unit -- nearly, but not quite! The centre of inertia of the large, stiff, straight and heavy tusk lies at some distance in front of the animal far from the propulsive force of its tail. With each powerful stroke of this tail, the animal not only throws itself forward, but turns or twists suddenly to one

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(*) Translator's note: PILLERI's translation (the ms from which I worked) of D'ARCY THOMPSON has "symmetry", which makes no sense. In THOMPSON's original it is "asymmetry".

side; but the mighty horn, attached only by its root, can, so to speak, react only with difficulty. This is so because at the thin base, the "coupling" by which it follows body twists, is at stressed, so that a "torque of inertia" arises. The horn does not twist with the animal in full synchrony, but the animal twists (so to speak) slowly and gradually about its own horn! The displacement due to the lag between the movements of head and tail is extremely small, but recurs with each beat of the tail. It manifests itself precisely at the growing root, the permanent pulp of the tooth, so sets up a stress, or exerts a torque at the exact site, and during the process of calcification.

Let us assume that at each stroke of the tail, lag between the rotations of tooth and body measures only one fifth of a second of arc, then this minute amount would be by far sufficient, taking into account a rough estimate of the age and activity of the animal, to explain all the spiralling seen on a tusk of medium size.

According to this explanation or hypothesis, the gradual twisting of the tooth corrects for any tendency to bend or curve in one or another direction; the grooves and ridges of the screw's "thread" are produced by irregularity and unevenness in the alveolus, which cause the "rifling" of the tooth during its growth. The coincidence in the direction [of rifling] in the two horns is thereby fully explained.

In spite of its own beauty, the spiral pattern of the tusk does not match the regularity or elegance of, for example, of a long, tapering *Terebra*, *Turritella* or any other spiral gastropod's shell. We assume that in the narwhal there exists only *overall*, but never exact correspondance between the rates of torsion and growth; because these two rates -- rate of translation and rate of rotation -- act separately and independently of one another, though their resultant remains fairly constant -- but no more than that. On the other hand, in the snail shell, actual tissue growth is the common cause of longitudinal and torsional changes during 51 growth, and the result is a perfect and regular spiral".

If we assume that THOMPSON hit the nail on the head with his theory, the following question arises: what other arguments may be adduced in its favor? According to THOMPSON, the spiraling of the tusk is a consequence of a special form of locomotion, common to all dolphins. But if one talks of locomotion, one must take into account those organs which subserve this activity, mainly tail and fluke. In all cetaceans, the fluke is triangular, with more or less angled anterior edges and a straight posterior edge.

This being the situation, I am astonished not to find any mention in North American and Canadian cetological literature of the fluke of the male narwhal, which differs from the typical [cetacean] shape. The only author to have remarked, in a very short note, on this particular fact is the experienced Danish zoologist, ALWIN PEDERSEN (1963).

h. The Fluke

If the shovel-shaped fluke of the adult male narwhal is 52 unusual, its postnatal change of shape, and the shape of the female's fluke, are no less astonishing. In short: the shapes of the flukes of the adult male narwhal, the juvenile male and the adult female all differ from one another (Pl.21). Let us first consider the ontogenic sequences of the male fluke. The fluke of embryos between 18 and 32 cm in body length (Fig. 16) is approximately heart-shaped, with a shallow caudal notch and well-rounded wings. In the bigger foetus of 132 cm body length, these have greatly enlarged in the latero-caudad direction. Thereafter, the wings grow in width; the anterior edges still slant caudo-laterally, while the posterior edges have become more horizontal and straighter. That is the fluke of juvenile males with one (or rarely two) short tusk (Fig. 17, 18).

Finally there is a latero-rostrad rotation of both of the fluke's wings, which produces the adult, shovel-like form. 53 The caudal notch has reached its greatest depth, the anterior edges are straight or have a slight rostrad concavity, the caudal margins are regularly rounded (Fig. 16). The fluke of the femal undergoes the same embryonal and foetal changes as those of the male, but in the adult retains the shape found in the juvenile male (Fig. 18,19). The fluke has broadened somewhat laterally, but its wings have not rotated forward, and even in old females the anterior edges of the fluke retain the

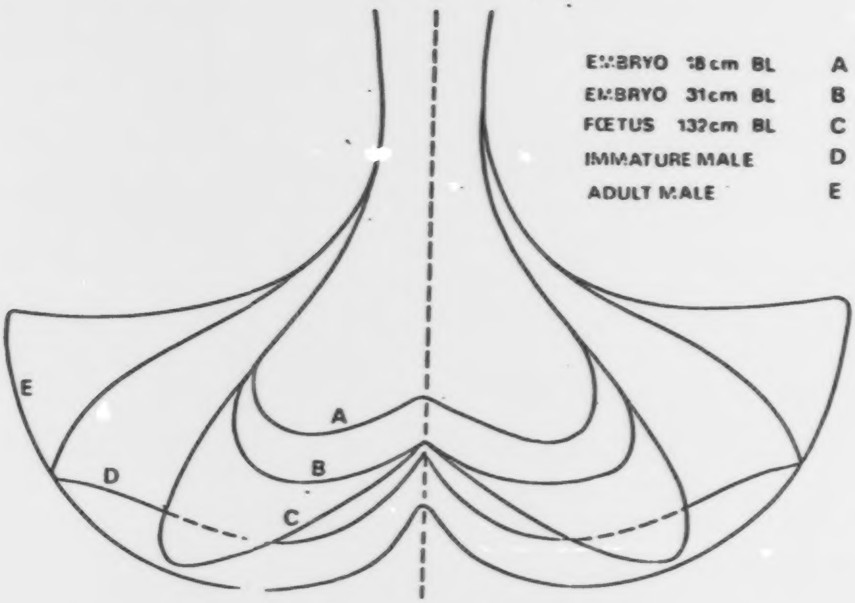

Fig. 16 Ontogenesis of the fluke of the male narwhal; dorsal aspect. Redrawn from photographs of captive animals.

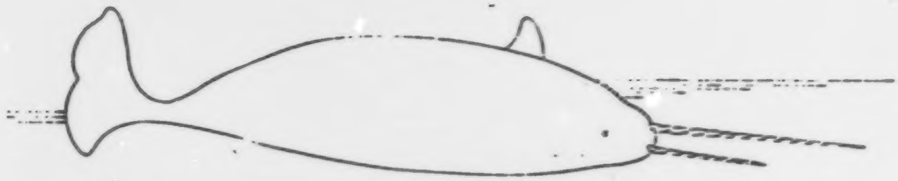

Fig. 17 Juvenile male with two tusks; body length = 372 cm. Observe the shape of fluke. Adapted from HAY (1980).

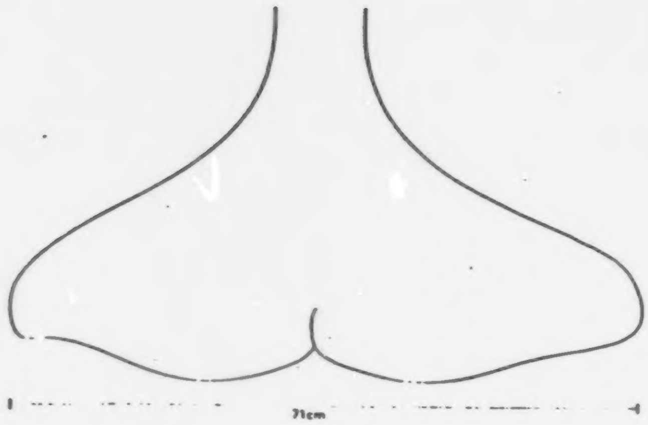

Fig. 18 Fluke of juvenile male from the exhibit collection of the British Museum (Nat. Hist.), London.

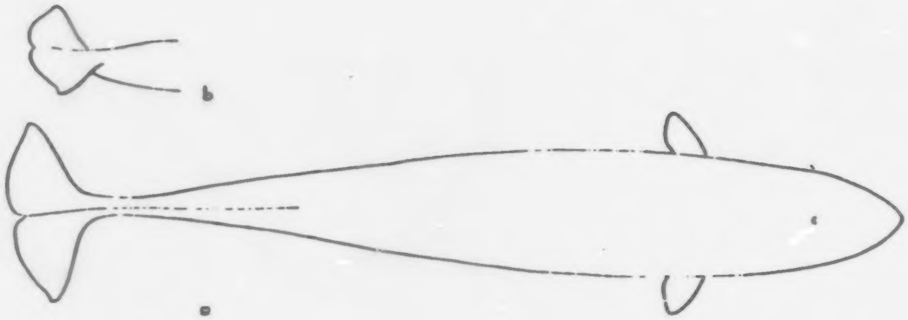

Fig. 19 Adult female narwhal. Observe the shape of the fluke. The animal stranded near Rainham, Essex, in 1949. (From information supplied by Dr. M. Sheldrick, BMNH, London, 1982).

latero-caudad slant.

In this connection, the narwhal's iconography in old zoological works is also of interest. Whereas the fluke of other species is usually shown as triangular, that of the narwhal is only sometimes shown as a triangle, at others, it has a shape characteristic of an adult male. In a drawing by SCHINZ (1824), which obviously was taken from the work of KLEIN (loc. cit.) (Fig. 20), a typical narwhal tail, with the wings of the fluke rotated forward, is tellingly, if exaggeratedly, represented. Still more extreme is the fluke in the drawing of LACEPEDE (1809) (Fig. 20). In comparing the various pictures in my collection, I get the impression that they may possibly represent narwhals of different ages.

One of the really remarkable developmental features of ontogeny and sexual dimorphism in the narwhal fluke is that the major phase -- i.e. the transformation of the generalized cetacean shape of the tail into the species-specific shape of the narwhal -- occurs, not in utero, but postnatally, during adolescence. What could have caused this, in phylogenetic terms, late evolution of the narwhal's fluke? When we compare the postnatal ontogeny of the fluke to that of the tusk, we see that the two correlate very well. In other words: it could 54
be the tusk that, by its growth, induces the fluke's shape.

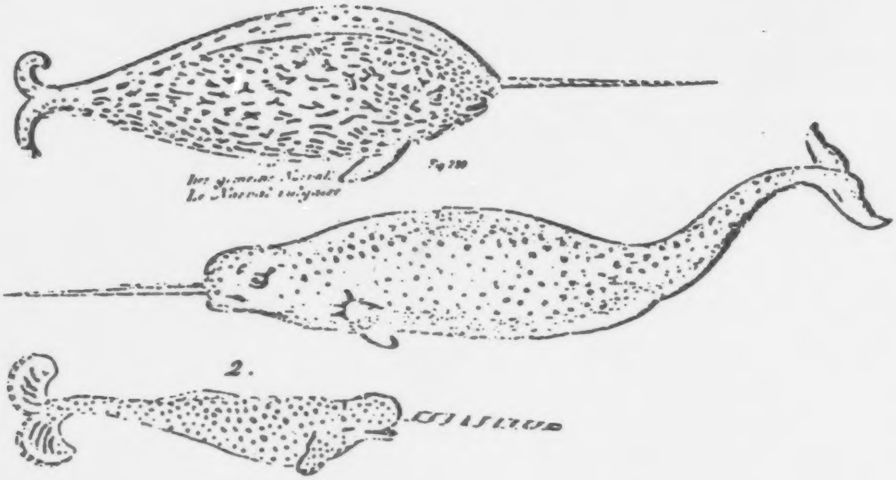

Fig. 20 Representations of narwhals. The two upper ones by SCHINZ, 1824; the lower, by LACEPEDE, 1809. (From the collection of G. PILLERI, Berne).

And -- because mature females have a male-"foetus" - type fluke -- a fully developed tusk would the conditio sine qua non of the peculiar species- and ... sex-specific shape of the narwhal male's fluke.

It was by chance that, on Pond Inlet, I was able to examine, in addition to a narwhal male, foetal stages of these cetaceans.

The obvious ontogenic dynamic of the fluke, and its correlation with the development of the tusk, mandate not only a morphological, but even more strongly a functional coupling between these two structures.

In view of this, our next questions are: (1) what effect could a fluke of this particular shape have on the way in which an adult male narwhal swims? (2) does the shape of the fluke allow us to reason backwards to an insight into the narwhal's method of locomotion?

It is well-known that in all whales and dolphins (including the narwhal) the caudal peduncle, which carries the fluke, is high, narrow and flattened on the sides. The great height of the tail is used to accomodate the strong muscles and mighty tendons which are responsible for the performance of the fluke. As HERTEL (1963) mentioned, this high pedunle can contribute little to forward motion when stroking vertically.

But because of the considerable lateral surface of the tail, horizontal strokes will be highly effective. When we calculate the static moment of the tail, we find that most whales and dolphins display approximately the same stroke effectiveness in the horizontal and vertical planes.

The static moment[1] provides a quantitative 55
indication of these relationships. Let us take Hertel's example of an 18 m[*] -long Sei whale (Blaenoptera borealis):

	A	B		C	D
	Teil	Fläche m^2		Hebelarm m	statisches Moment m^3
E	Flosse	3.3	×	5.8	19
F	Träger	4.5	×	1.9	8.5
G	Dorsalsicht	7.8			27.5
H	Lateralsicht	9.5	×	2.9	27.5

I $\frac{\text{Moment (Flosse/Träger)}}{\text{Moment Seitenansicht}} = \frac{27.5}{27.5} = 1:1$

For translation of legends A - I, see next page.

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(1) I thank my assistant, Dr. M. Ghir, for the calculations.

(*) Translator's note: The ms gives "18 cm", which is obviously a typographical error.

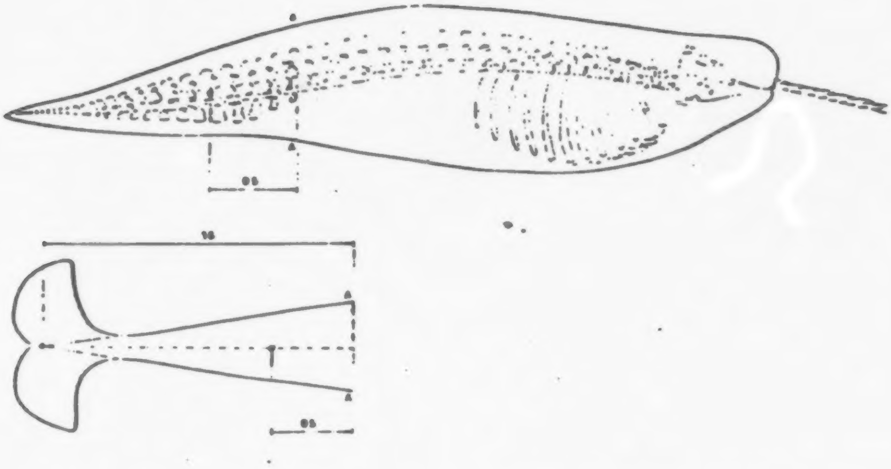

Fig. 21 Calculation of the static moment of the tail (fluke + peduncle) in an adult, male narwhal.

A = component B = area (m^2)
C = lever arm (m) D = static moment (m3)
E = fluke F = caudal peduncle
G = dorsal view H = lateral view
I = Moment (fluke + peduncle)/ Moment (side view)

For the narwhal tail (Fig. 21), on the other hand, the following values have been calculated:

	A	B		C	D
	Teil	Fläche m^2		Hebelarm m	statisches Moment m^3
E	Flosse	0.3	×	1.6	0.48
F	Träger	0.4	×	0.5	0.20
G	Dorsalsicht	0.7			0.68
H	Lateralsicht	0.6	×	0.5	0.3

I $$\frac{\text{Moment (Flosse/Träger)}}{\text{Moment Seitenansicht}} = \frac{0.68}{0.3} = 2.2:1$$

Further, as a comparison, these are the results of calculations on the Indus dolphin (Platanista indi; body length = 1.3 m), which swims on its side:

	A	B		C	D
E	Teil	Fläche m^2		Hebel-arm m	statisches Moment m^3
E	Flosse	0.012	×	0.45	0.00596
F	Träger	0.038	×	0.12	0.00467
G	Dorsalsicht	0.051			0.0106
H	Lateralsicht	0.054	×	0.11	0.006

I $\frac{\text{Moment (Flosse/Träger)}}{\text{Moment Seitenansicht}} = \frac{0.0106}{0.006} = 1.8:1$

When one compares static moments in the three cetacean species, one can clearly see that, in the narwhal, the tail's horizontal stroke contributes far less to propulsion than the vertical stroke; in fact, its share is even less than in the Indus dolphin, which swims on its side.

Furthermore, in species with a deep caudal peduncle (Tursiops) one must consider the possibility of a twisting 57
motion of the tail about its long axis. Thus, propulsion in cetaceans depends on the combination of three wave motions:

1. the vertical stroke, making special use of the fluke;

2. the horizontal stroke, exploiting the large lateral surface area of the tail;
3. the screw-like twisting about the long axis.

Points (2) and (3) remain entirely unexplained because we lack both observations of the living narwhal and films of its swimming. However, we can assume with much certainty that, among the cetaceans, the dynamics of the narwhal's tail are unique.

If we now reconsider the spiraling of the tusk, which we may want to look upon, in THOMPSON's (loc. cit.) sense, as a direct result of the body's rotation about its long axis, then we do not lack supporting evidence.

The torpedo-shaped body of the narwhal does not have a dorsal fin, an appendage which first of all protects an animal against rolling about its own axis. Instead of such a fin, the narwhal has a broad, keel-like ridge, with rounded edges, which occupies about 2/3rds of the length of the body. The pectoral fins are small, but relatively solid in build. The eyes are placed well to the side so that the visual field of each eye is oriented mainly laterad. This allows the narwhal -- when lying on its side -- to see objects both in the depths of the ocean and at the surface of the water, i.e. at the underside of the ice cover.

We shall remain ignorant of the feeding behavior of the narwhal until we manage to observe adult males catching ground-fish in the aquarium.

But when we consider both the position and small size of the mouth opening, and the far ventral insertion of the tusk, we can imagine that catching such prey (e.g. rays, halibuts) will be easier when the whale is on its side than when it is belly-down.

If the tusk has grown on the left, or usual, side, then lying on the right side would no doubt be a far better position for grasping prey with the jaws.

If the narwhal attempts to catch its prey while in the belly-down position, the tusk will have to be much closer to the bottom, and more nearly parallel to it, than if he were on his side; the body will also have to be in opisthotonos. I believe that it is just such problems in catching ground-fish, some of which may live on rocky bottoms (*Acanthocottus*), that could account for the tusk-fractures which PORSILD and other zoologists have noted.

This would mean that the narwhal, when feeding on the bottom, would have to rotate on its body axis.

When one compares torque at the lateral aspect of the
caudal peduncle with that at the horizontal surfaces of the
peduncle and fluke, it becomes evident that, in the narwhal,
as opposed to other species, the latter is far greater.
Considering the hydrodynamics involved, such a morphological 58
arrangement would be by far the most advantageous for rotations
about the body's axis.

It is possible that the effect of such rotations, when transferred to the tusk, might explain the latter's spirals.

But quite apart from the still hypothetical feeding behavior of narwhals at the sea bottom, rolling has often been observed at the surface by NANSEN and particularly by DEGERBØL and FREUCHEN (loc. cit.). Unfortunately, these authors did not report in which direction the animals turned.

I fully understand that these preliminary results are far from sufficient to allow useful conclusions concerning the hydrodynamics of tail fin and locomotion in the male narwhal. But they do point out problems and the way to future research.

In addtion to ethological, cinmatographic and physical studies, we will need the kind of rigorous structural analyses of muscle fiber directions and tendon insertions in the fluke that ROUX (1895) and PURVES (1963, 1969) made in Phocoena phocoena. I am quite certain that the results of such work will also shed more light on the nature of the tusk.

It may further be relevant to my studies that aeronautic engineers have built planes with wings that have negative sweepback, (i.e. point forward), and others with wings having positive sweepback, but tail assemblies with negative sweepback. Aerodynamically, the fluke of the narwhal represents the negative sweepback type. This is, no doubt, another point of view that might be considered when studying the physics of this appendage.

i. Sonar Sounds and Sonar Field

There are only a few, sporadic studies of the pulsed, or sonar, sounds of the narwhal; from these one can not elicit either the exact form or the frequency spectrum of the clicks. The rich area of the whale's repertory of low-frequency sounds has been investigated even less. Nearly all field observers of the past describe, among other things, narwhal sounds. In these instances, the sounds are breathing noises, made when the whales surface, and not those sounds that are produced under water.

The pharynx of the narwhal is, like that of all other ceWaceans, the sound-producing organ (PILLERI, 1983).

In an earlier work (PILLERI*et al.*, 1982) we tried to derive, from theory, the shape of the sonar field as determined by the structures of the skull.

These studies showed that the sonar field consists of two overlapping segments: a frontal sector and a ventral one that is beamed through the region of the throat towards the bottom. The ventral segment of the field is due to incomplete screening of the pneumatized pterygoid sinuses (Pl. 22), which leave, at the base of the skull, a median opening, known as the pterygoschisis[*] (PILLERI, 1981).

Looking at the frontal sonar field and considering 59
the spatial distribution of the high frequency signals, one notes that the location of the male narwhal's tusk is near the axis of this sector of the field, in the zone with the highest sound energy.

Under these circumstances, it is impossible to exclude the tusk from any system concerned with the conduction of sound. The sound produced by the larynx propagates itself *via* the wall of the nasopharynx (lower choanae) and the palatopharyngeal muscle to the rostrum of the skull (vomer and its cartilage, premaxilla and maxilla) and thence to the skin. In the narwhal, the tusk and its root lie remarkably close to the palatopharyngeal muscle and to the larynx, and coupling with the above named structures is continuous (see Pl. 20).

(*) Translator's note: misspelled "Pterygoschis" in ms.

That is why I am much surprised that DOW and HALLENBERG (loc. cit.) in their work on the tusk's pulp contend that "the absence of lipid cells and tissue ... eliminates the possibility that the narwhale tusk contains bioacoustical lipids useful in echolocation", and thus deny that the tusk migth have any part in the functioning of the acoustic system.

Today we know that the "acoustic" lipids (isovaleric acid) have absolutely nothing to do with acoustics. They were found in the melon of some cetaceans (e.g. Tursiops), but the melon has no role in the acoustic system (PILLERI et al., 1983; PILLERI and PURVES, 1983).

The tusk consists of a type of ivory that is much denser than the compact zone of the premaxilla, and even though, so far, no sound measurements have been made, one must assume that the tusk conducts sound waves, and in particular supersonic ones, with extreme ease. But it is also clear that the small size of the tip of the tusk prevents the tusk itself from beaming-out oriented sound waves.

In normal teeth, in which the density is 3,000 and the velocity of sound conduction 5,400 m/sec, the impedance is calculated to be 10×10^6. One must assume that the values of these parameters will be even more advantageous in the narwhal tooth.

After this discussion of the basics, we must consider how the narwhal may integrate the sonar system with its special environment.

While other cetaceans beam their locating signals at an open-water surfce, the waves of which send back sharp echos, the narwhal has to face an ice-covered surface for at least half of the year. This ice-cover can lock up most of the whale's winter habitat, as one can see from the sassvats: clearly the narwhal is excellently adapted, as no other cetacean species, to obviate this "danger" from above.

It is not easy to study Arctic animals during the winter months in the region of the pack-ice; in fact, special means of transport are required when the study deals with amphibious or marine animals. It is mainly because of these difficulties that our knowledge of the narwhal's behavior in 60
winter is so scanty.

One of the first problems to be addressed will be to discover how the narwhal's sonar system functions under the ice cover. For this, we need to know the characteristic characteristics of the ice's lower surface. This surface, which faces the water, is smooth in fresh-water lakes that freeze over in the winter[1].

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(1) Mr. Hermann J. Gruhl, underwater photographer in Albstadt, whom I consulted in this matter, reported:
1. The underside of the ice is usually entirely even and mirror-smooth, never wavy, though waves too large to recognize

Usually, they are quiet waters, without waves. In the ocean the situation is different; the underside of the ice may be smooth, if it formed in a quiet bay or isolated fjord. Elsewhere, the underside of the ice has waves, usually from 10 to 100 cm long, and shallow (MOSETTI, personal communication).

It has sometimes been observed in sassvats that the whales broke open the ice cover with the melon[1] in order to make breathing holes, even if the ice was up to 15 cm thick (PORSILD, loc. cit.). One must assume that before delivering its blow, the animal was able to estimate the thickness of the ice. Seen from above, young, thin ice is bluish, whereas older, thicker ice becomes white. It is possible that the narwhal may be able to perceive differences in thickness by assessing differences in light intensity, or transparency optically, by sight. But light conditions during the arctic winter, particularly on moon-less nights, are poor. Such considerations lead me to believe that the narwhal may be able to probe the ice by means of sonar, and to obtain exact information on the thickness of ice from the echos. In ice,

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(1) I am inclined to believe that they use their backs to break open the ice.

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with the unaided eye could possibly exist.

2. Air bubbles may be trapped in the ice; in these circumscribed areas, the underside of the ice may be uneven and quite rough to the touch.

3. The water level usually sinks in winter. The ice cover then sinks together with the receeding water level, producing rifts and faults along the underside of the ice. Even cracks right through the entire ice-cover are then not unusual. These subsequently freeze shut again, but an unevenness persists.

the speed of longitudinal sound waves is 3,980 m/s. Here is a broad field for biological and technical research in acoustics.

I briefly mentioned above that in addition to the rostral sonar field, the narwhal also produces a broad ventral one. In this respect it much resembles beluga, the species most closely related to the narwhal.

Certain anatomical peculiarities may be of interest in this connection: the structures of the skull that lie rostrad from the larynx and are concerned with the generation of near (= interference field) and far fields (see PILLERI *et al.*, 1983) show perfect symmetry. This is in sharp contrast to the considerable asymmetry of the epicranial region (premaxillary
trigone, superior choanal orifice, nasal structures). Because 61
of this, one might expect the sonar field -- in spite of the sinistral location of the tusk -- to be symmetrical.

High frequency sound waves originating in the larynx give rise to the best echolocation information and are highly directional in cetaceans; low frequency waves, on the other hand, are increasingly less directional and provide less information through their echos. In whales and dolphins the sonar fields are fixed in space and one wonders how the animal uses its sonar, i.e. how it orients its toothed head and its body towards the target to be explored.

Future research should attempt observations of the swimming behavior of these cetaceans under the ice in order to obtain some idea about echolocation under pack ice. So far, we shall have to make do with hypotheses.

If the animal should approach an edge of ice, or a small polynya in the vertical position (Fig. 22), there would be no difficulty in obtaining clear echos from the surface.

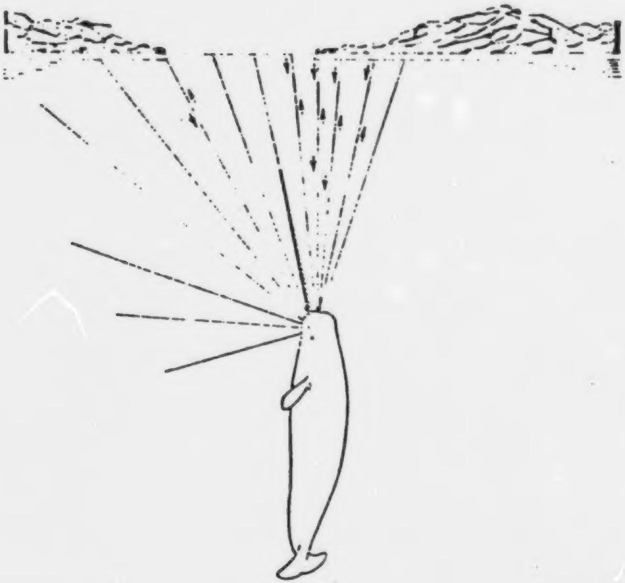


Fig. 22 Hypothetical representation of narwhal echolocating in a small polynya in pack ice.

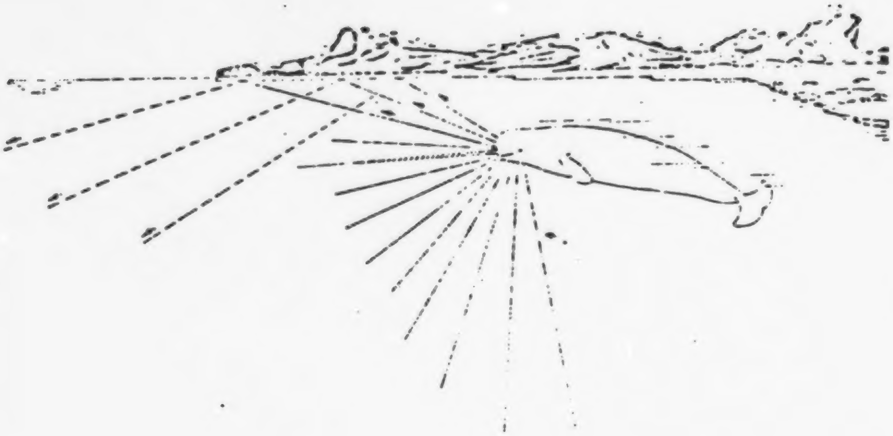


Fig. 23 Narwhal in normal (belly down) swimming position echolocating at a smooth pack ice undersurface. Hypothetical representation of the sound waves.

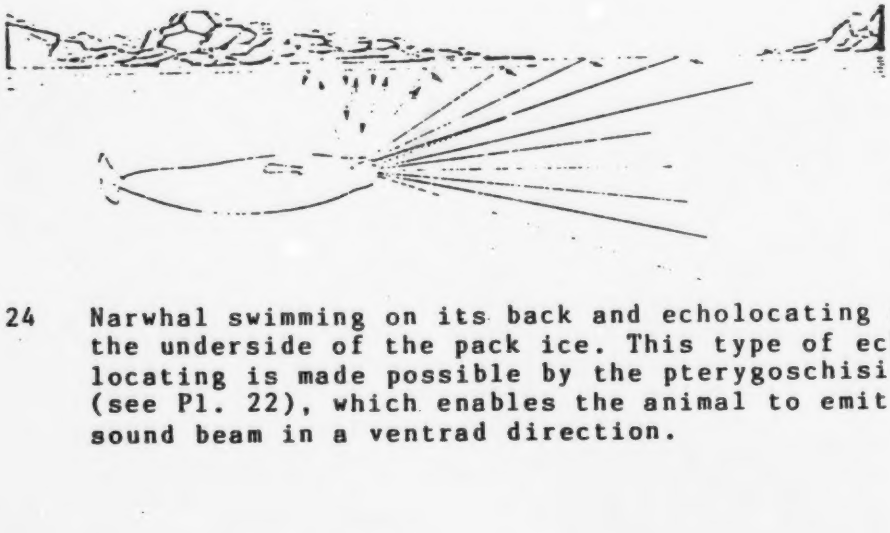


Fig. 24 Narwhal swimming on its back and echolocating at the underside of the pack ice. This type of echolocating is made possible by the pterygoschisis (see Pl. 22), which enables the animal to emit a sound beam in a ventrad direction.

But let us assume that the ice cover is entirely smooth and that the narwhal is swimming parallel to it; then there would be an echo from sound waves of the rostral field sector impinging at an angle onto the ice surface (Fig. 23). Now a turn about its axis would let the animal bring into play the ventral sector sonar, vertically to the ice, and so get sharp echos (Fig.24).

I should like to stress that my ideas and the 62
sketches that are appended are still very much hypothetical. Their purpose is to stimulate in-the-field ethological observations. Today, even in the arctic, it is possible to use diving as a research tool; a second possibility would be to introduce a periscope under the ice. Best, however, would be a mini-sub. But these are unfortunately very expensive pieces of equipment. Much less expensive, and possibly more revealing would be long-term observations of a savssat, during which one would have to prevent killing and disturbing of the animals by the Inuit.

A final word concerning echolocating sounds, or clicks. So far, narwhal clicks have not been rigorously analyzed, nor has one so far been able exactly to establish the position of the animal relative to the hydrophone during the recordings. In view of the directional characteristics of the sonar beam, this would be an important prerequisite for click analysis.

In spite of this deficiency, I am certain that clicks of the narwhal resemble those of beluga. In my classification, the are of Type II, i.e. signals with two frequency ranges, one high frequency, the other low frequency. Even in the absence of concrete data, one could predict that the narwhal would produce this type of click, simply from consideration of the specific anatomical relationships in the region of larynx and palatopharyngeal muscle. The part of the muscle that surrounds the larynx like a sphincter stretches ventrally between the two pterygoid hamuli, which do not make contact in the median line. As in beluga, there arises a pterygoschisis (Pl. 22), and the incomplete pneumatization at the pterygoid sinus makes it possible for the laryngeal sound to radiate out in a ventrad direction through this opening.

It is most likely that the part of the muscle that is not in contact with the bone produces the low-frequency component of the click.

Inasmuch as larynx and palatopharyngeal muscle form a functional unit, the two frequency components of of the click are sent out synchronously.

DISCUSSION

In the preceding chapters I could only touch upon a very few problems concerning the biology of the narwhal, and discovered more unanswered questions than answers. If one tries to establish a balance sheet of our present knowledge concerning this particular whale, one finds that in spite of a fairly extensive literature, the real study of this peculiar denizen of the Arctic has not actually, or at least hardly, begun.

The majority of morphological studies are restricted to macroscopic observations, and it is only in the past few years that histological studies on the structure of tissues (pulp of tusk; retia mirabile) have begun. None of the sense organs, in particular none of those that best mirror the characteristic adaptations to the Arctic environment, has been analyzed in depth. Insofar as ontogeny is concerned, only one early stage has been examined, and even there, just the head. The development of the tusk, however, is better understood, particularly in regard to the determination of age.

The chemical compositions of blood, urine and body fluids are practically unknown.

The narwhal is an echolocating animal, but so far we know very little about its sonar system. At what frequencies does it emit sound, and how do the sound waves behave in ice? How much of the sound energy is reflected; how much absored in the medium? What do the echos look like?

So far, none of the research work has described
the low frequency sounds of Monodon; no one has correlated
them with specific behavioral situations, nor tried to find 64
homologies between them and the sounds made by other whales.

There are no long-term, systematic, ethological studies, and we know more about the mythology of the tusk than about its biological significance ... a list of the still unresolved questions for research to answer could fill whole pages.

During the past decade, people have, with much justification, become concerned about the survival and protection of the narwhal. But we shall not be able to provide effective protection until we know more about the natural history, and, first of all especially the psychology, of this species. The level of development of the central nervous system and the high degree of differentiation of the narwhal's brain suggest that the animal represents a psychologically well-advanced species.

This should stimulate our scientific curiosisty, and should also imbue us with reverence and incite us to reflection.

SUMMARY

On a voyage to Baffin Land, the author was able to collect anatomical specimens of the narwhal (Monodon monceros L.) for his studies and carry out initial observations concerning these cetacea. In addition to conveying brief travel impressions of Baffin Land and the Inuit population in Pond Inlet, this report attempts to provide an idea of the present state of research on the narwhal and points to specific features which reflect the particular ecology of this animal. In Baffin Land, specimens of the eye, the hearing organ, the central nervous system, the air sack system and the tusk were collected in particular.

Monodon is a monospecific Pleistocene genus confined to the Artic; there is no Miocene evidence. Its evolution (speciation) must therefore have been very rapid, tachytelic.

The brain of the adult male weighs 2605 grams. Its differentiation suggests a high mental capacity.

The eye is placed laterally, a position which rules out a binocular field of vision. There is no Operculum pupillare.

The N. acusticus is the largest brain nerve, exceeding - in contrast to Beluga, Delphinapterus leucas – the N. trigeminus in size. Compared with that of Beluga and Delphinus delphis, the N. trochlearis is appreciably reduced.

In the narwhal, the hearing organs are very well formed. The Meatus acusticus externus is functional and is actuated by several muscles. The ossicula, particularly the incus, are well developed, more so than in other cetacea, and indicate no retrogression. The weight is six times greater than in Homo sapiens.

The rigid anchoring, extending to ankylosis of the stapes at the oval window and the incus at the bulla wall does not argue for non-functionality in sound transmission; it rather suggests the capacity to transmit supersonic sound waves from the tympanic membrane to the labyrinth. Both the resonance theory and the concept of direct bone transmission circumventing the ossicula of the middle ear are false.

In the narwhal, orientation and other sounds are produced exclusively by the larynx. The sonar field is both rostrally and, owing to pterygoschisis, ventrally directed. The tusk is located in a region of the sonar field with the highest sound energy; due to its relative narrowness, however, it has no effect on the directional characteristic of supersonic waves. According to the structure of the pterygoid sinus, the narwhal would be expected to produce a complex click with two synchronous frequency components as Beluga does. The efficiency of echolocation in the narwhal with reference to the ice conditions (reflexions, absorption, velocity of sound, transmission coefficient, etc.) has not yet been studied.

The tusk is the most remarkable feature of the narwhal. Concerning the formal genesis of the left-hand spiral, the earlier theory of d'Arcy Thompson to the effect that the swimming pattern might be responsible for emergence of the cement spiral, is again gaining currency. On the basis of these ideas, attention was given to the

form of the tail. Adult males with a fully developed tusk display in a tail fin shape which is fundamentally different from that of adult females, younger males or other cetacea. Hydrodynamically seen, the fin is negatively sagittate with regularly rounded back edges. It is significant that this tail fin takes its final shape post-natally and at a very late stage and not until the complete maturity of the tusk.

This feature cannot be attributed to a sexual dimorphism; it is rather the result of the particular mode of locomotion of the adult male narwhal. In this respect, significance also attaches to the fact that the static moment for the lateral surface of the bearer has a much lower value than that of the dorsal surface of the same radial plus fin. The relation of the two moments in the narwhal is even more extreme than in the blind Indus dolphin (Platanista indi), which is a side swimmer.

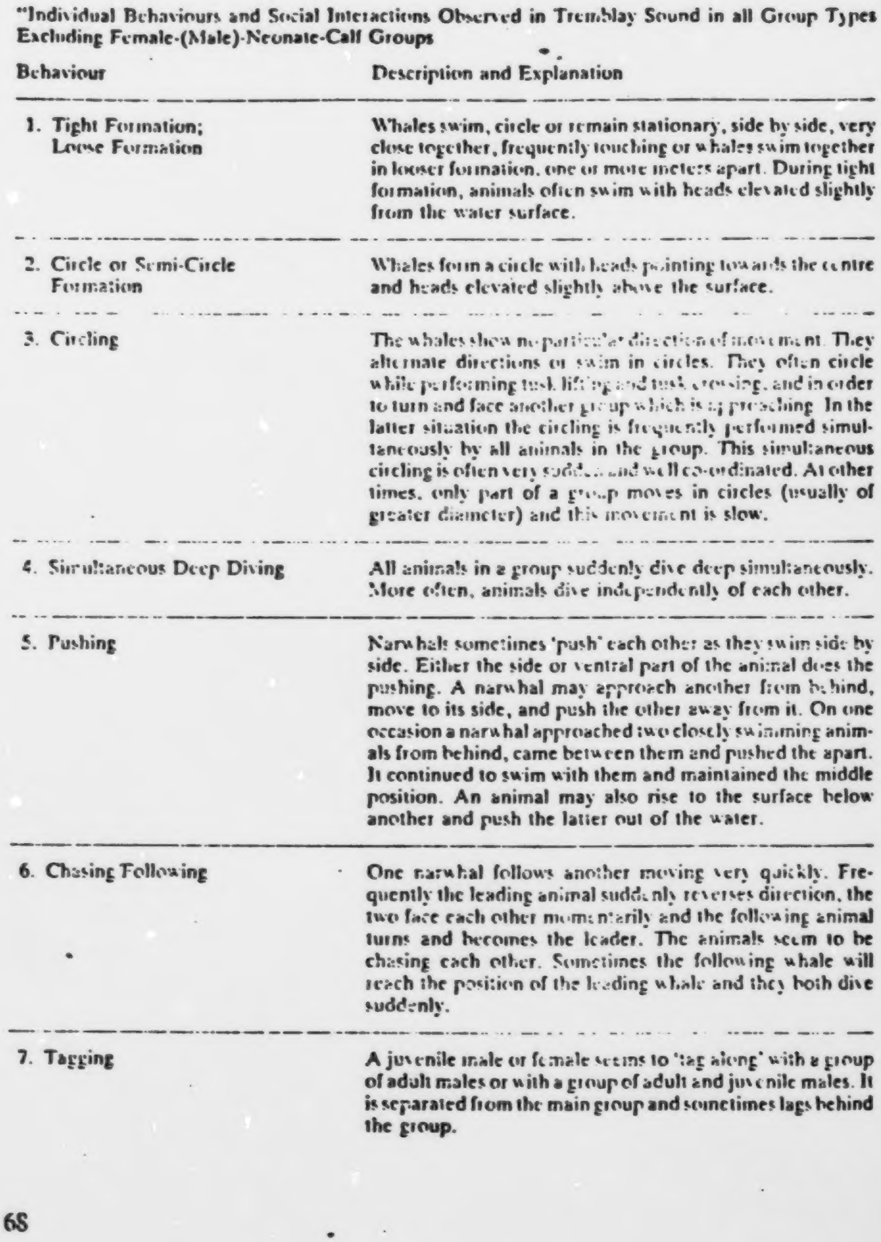
The functional importance of these features should be confirmed by observation of the swimming posture and hunting behaviour of the narwhal in the Arctic seas.

With regard to other behavioural aspects, the author considers that the polynia (Savssat) kept open in the ice by narwhals is an ordinary case of synaporia.

ADDENDUM

It was not until after this paper had gone to press 67
that I received from Canada an unpublished doctoral thesis out McGill University concerning the narwhal. The research paper was entitled *"Social Organization and Behaviour of the Narwhal, Monodon monoceros, L., in Lancaster Sound, Pond Inlet and Tremblay Sound, Northwest Territories"*(Montreal, 1979), by HELEN B. SILVERMAN. It is an extremely sound study, which in my estimation contains more information about the ethology of this cetacean than all the prior publications of an entire century. Which is why I regret that this work has been available for dicussion only to a restricted audience and has not been made available to a wider public. HELEN SILVERMAN has summarized her observations as follows:

The following Table 17 (loc. cit., p. 67) summarizes the individual behaviours and social interactions of all groups, except the Female-(Male)-Neonate-Calf group.



"Individual Behaviours and Social Interactions Observed in Tremblay Sound in all Group Types Excluding Female-(Male)-Neonate-Calf Groups

Behaviour	Description and Explanation
1. Tight Formation; Loose Formation	Whales swim, circle or remain stationary, side by side, very close together, frequently touching or whales swim together in looser formation, one or more meters apart. During tight formation, animals often swim with heads elevated slightly from the water surface.
2. Circle or Semi-Circle Formation	Whales form a circle with heads pointing towards the centre and heads elevated slightly above the surface.
3. Circling	The whales show no particular direction of movement. They alternate directions or swim in circles. They often circle while performing tusk lifting and tusk crossing, and in order to turn and face another group which is approaching. In the latter situation the circling is frequently performed simultaneously by all animals in the group. This simultaneous circling is often very sudden and well co-ordinated. At other times, only part of a group moves in circles (usually of greater diameter) and this movement is slow.
4. Simultaneous Deep Diving	All animals in a group suddenly dive deep simultaneously. More often, animals dive independently of each other.
5. Pushing	Narwhals sometimes 'push' each other as they swim side by side. Either the side or ventral part of the animal does the pushing. A narwhal may approach another from behind, move to its side, and push the other away from it. On one occasion a narwhal approached two closely swimming animals from behind, came between them and pushed the apart. It continued to swim with them and maintained the middle position. An animal may also rise to the surface below another and push the latter out of the water.
6. Chasing Following	One narwhal follows another moving very quickly. Frequently the leading animal suddenly reverses direction, the two face each other momentarily and the following animal turns and becomes the leader. The animals seem to be chasing each other. Sometimes the following whale will reach the position of the leading whale and they both dive suddenly.
7. Tagging	A juvenile male or female seems to 'tag along' with a group of adult males or with a group of adult and juvenile males. It is separated from the main group and sometimes lags behind the group.

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8. Forward Somersault, Rolls, and Upside Down Swimming	The whale dives, but instead of continuing forward motion its head and body move down and then back so that it is upside down (underwater). From this position, its head and body move up and then forward to the dorsal side up position in which it began. Sometimes the animal will do a half somersault so that its final position is upside down. To right itself, it simply rolls over. Half lateral rolls, complete rolls, and upside down swimming were also observed.
9. Tail Slap	The tail is raised and slapped against the water surface. The whale's body is usually underwater when performing this behaviour.
10. Flipper Slap	While swimming slightly on one side, the flipper, which is just above the water surface is moved up and down against the surface causing splashing.
11. Tusk Slap	The head and tusk are lifted above the water surface and brought down hard upon the surface.
12. Breaching	A narwhal swimming quickly underwater, either on its side or dorsal side up, lifts itself out of the water on an angle so that only the caudal peduncle and the tail remain underwater, and then falls back into the water. This was observed rarely.
13. Head Down Position	The tail lies flat on the surface while the body and head are angled downward in the water. This same position may also be performed with the tail raised above the surface or the body may be horizontal at the surface with head (and tusk) pointing down. Other whales in the group may or may not also be in this position.
14. Head Up Position	The head is elevated above the water surface on an angle, from slightly above the surface to a vertical position. If the narwhal is a male, the tusk will also be above the surface. Sometimes the body of the narwhal protrudes from the water as far as the level of the flippers and the head and tusk are waved back and forth. This is probably caused by swift back and forth movements of the tail in order to maintain this position. Other whales in the group may or may not also be in this position.
15. Piggyback	One or more narwhals swim over or lie transversely upon the back of another. Up to four narwhals have been seen lying on the back of another. The bottom animal may also be upside down while the animal(s) above lie on its ventral side.
16. Head Over Head	The head of one narwhal is placed over the head of another or two narwhals are side by side in V-formation with heads touching. The ventral surface of the head is also sometimes placed over the tusk base of a male.
17. Head on Caudal Peduncle	The head of one whale is placed across the caudal peduncle of the whale below. On one occasion, the whale below simultaneously raised its tail from the water.

18. Tail Brush	The tail is brushed against or touches another whale.
19. Head On Approach	Two or more narwhals face or approach each other head on. Sometimes one or both of the approaching whales elevate the head and tusk from the water. Upon meeting, the approaching whale(s) either turns so that it is side by side with the other or it dives under the other whale(s). When two groups or subgroups approach, one usually dives under the other.
20. Tusk Pointing	The head and tusk are turned and pointed towards another whale. There is no physical contact. Sometimes two males swimming side by side in loose formation will simultaneously turn their heads and point their tusks at each other.
21. Tusk Up Position	A male is positioned vertically or on an angle below the water surface with part of the tusk protruding above the surface. Often only the very tip of the tusk is visible. On occasion, one or more narwhals in this position will alternately rise and sink several times varying the degree to which the tusk is exposed above the surface.
22. Upside Down Tusk Raise	The narwhal is in an upside down horizontal position. The head is then raised upwards, lifting the tusk into the air until it is almost vertical. Sometimes the head is waved back and forth.
23. Bent Position	A male is positioned almost vertically underwater with the neck bent so that the tusk in in a horizontal position at the water surface. The dorsal surface of the head is up.
24. Tusk Contact Avoidance	As one male approaches another narwhal, the approaching male points its head and tusk down or to the side, thereby avoiding tusk contact.
25. Tusk Crossing	There are many variations of this behaviour: (a) Two males positioned horizontally side by side bring their tusks together and touch or cross the tusks momentarily. Often just the tusk tips come into contact. (b) Two or more males face each other with heads just slightly elevated from the water, and cross tusks. (c) Three males or two males and a female lie horizontally at or just under the water surface, side by side. The two outside males turn slightly towards each other and cross their tusks. The middle animal is usually not involved in the tusk crossing either because it is a female, it is a very young male with a small tusk, or it is an older male whose tusk is pointing down. This behaviour also occurs without a middle animal. (d) Two or more males elevate their heads and tusks from the water and cross tusks. As in (c), a centre animal may be present, which is not involved in the tusk crossing and lies horizontally at the water surface (Figs. 25 a-c). (e) Two or more males with bodies angled downward and heads and tusks pointing down cross tusks.

	(f) One male places its tusk over the tusk of another. Males lie horizontal and perpendicular to one another. Circling frequently occurs while in this position. (g) One male is at the surface. Another is positioned vertically underwater with the upper portion of its tusk above the water surface. The tusks are in contact (Fig. 25). (h) Males repeatedly cross and uncross tusks and change tusk positions. For example, a male with its tusk below that of another, places its tusk above. (i) One male lifts its tusk to touch or cross the tusk of another male which is already elevated. Tusks were observed to be crossed in the following positions: tusk tip over tusk base; tusk tip touches mid-tusk; ventral mid-point of one tusk over dorsal midpoint of another tusk; two tusks crossed halfway between their bases and midpoints; ventral tusk base over dorsal tusk base; ventral part of tusk over lateral part of tusk.
26. Tusk Pushing and Jerking	(a) Animals lie horizontally side by side and cross tusks. The male with tusk above seems to push down on the tusk below. The tusks seem to slide or move against each other. The male with tusk below suddenly jerks its tusk downwards. (b) Three males lie horizontally side by side. The two outside whales are at the surface while the middle whale is slightly below. The bodies of the two outside males are in contact with that of the middle male. The two outside males have their tusks crossed over the head of the centre male. Tusks are horizontal at the water surface. While maintaining the position of the tusks, both whales elevate heads and tusks above the surface. It seems that the whale with tusk positioned below pushes up the tusk of the other. This latter male then seems to push the tusk below back into the water in a sudden and quick movement. Some tusk along tusk movement is observed. The centre animal remains motionless. (c) A male raises its tusk at an angle of about 30° to the water surface and brings it down hard onto the tusk of another male. The tusks separate and cross again more lightly. (d) One male touches the tusk of another male with its tusk. The latter male jerks its head to the side. (e) Two males touch tusk tips and immediately jerk their heads away from each other.
27. Head Shaking	The head and tusk are shaken vigorously from side to side by one or more males while lying in a horizontal position at the water surface.
28. Tusk-Body Contact	(a) The tusk of a male momentarily and lightly touches part of the body (e.g. head, back, side) of another narwhal. (b) The tusk is placed over the back of another narwhal. (c) A male is positioned vertically underwater. It uses its tusk to 'lean' against the side of another whale which is positioned horizontally.

29. Tusk Rubbing	The tusk is used to 'rub' another whale over its blowhole region and along the back, head, side, and tusk. On one occasion a male slid its tusk along the tusk of another male from the tip towards the base and up over the head while the male below slightly lowered its head and tusk. Another example of 'tusk rubbing' is shown in Fig. 25.
30. Arching	(a) A male arches its anterior back and jerks its head upward out of the water and down. (b) Two males in a horizontal position at the surface are in a V-formation with tails touching. They both arch their backs out of the water.
31. Falling Down	An animal in the vertical position (head up) falls down upon another whale lying in the horizontal position.
32. Bubble Blowing and Vocalization	Bubble blowing (air emitted underwater) was observed during many of the above behaviours. This may be associated with vocalization. On one day, many vocalizations (clicks, whistles, moans) produced by whales performing some of the described behaviour were clearly heard from the observation site (305 m elevation)
33. Female Aggression	This sequence of behaviour was observed only once and seemed to be the most direct, aggressive behaviour exhibited. An adult female was accompanied by two juveniles (sex unidentified). She turned her head very sharply towards one of these juveniles and began to open and close her mouth very quickly while moving her melon quickly up and down. Suddenly she rolled onto her side, swerving her head towards the juvenile and hit it hard with her mouth on its midlateral side. Then all three dove deep. During most of this sequence the melon was continuously moved up and down and at times the tail and head were flexed upwards.

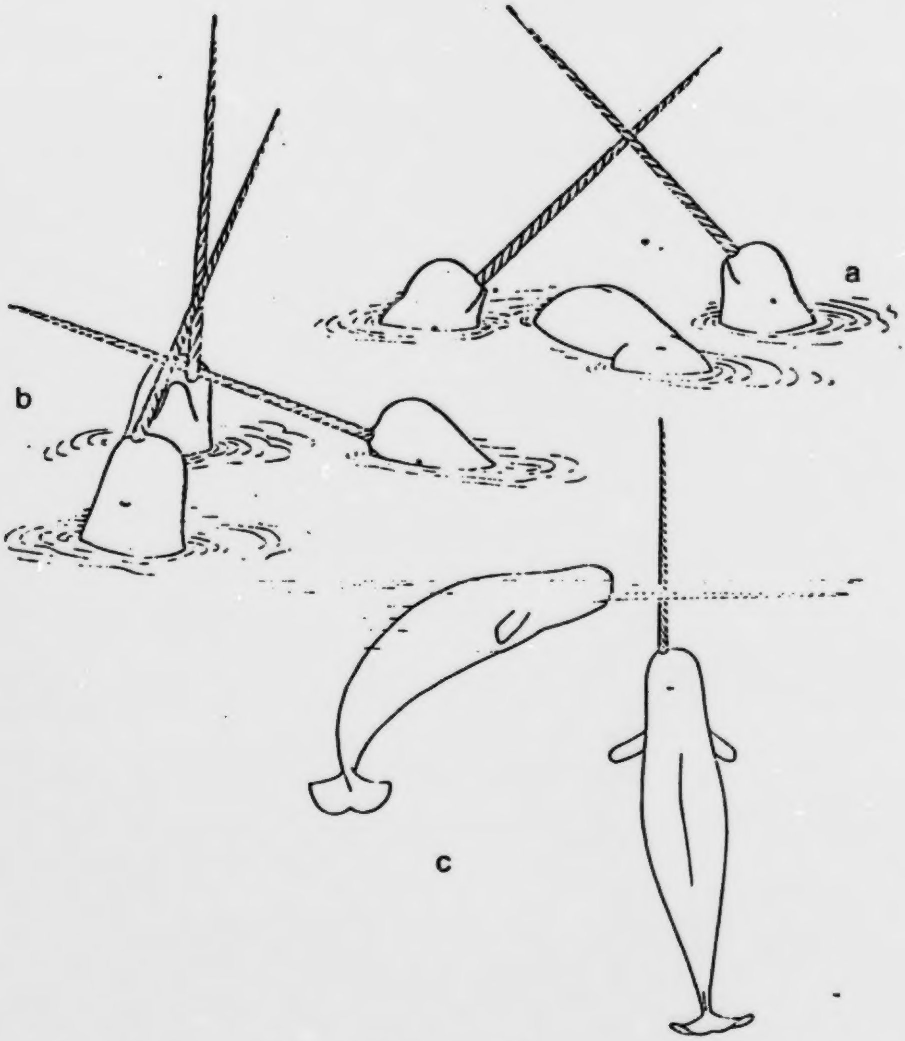
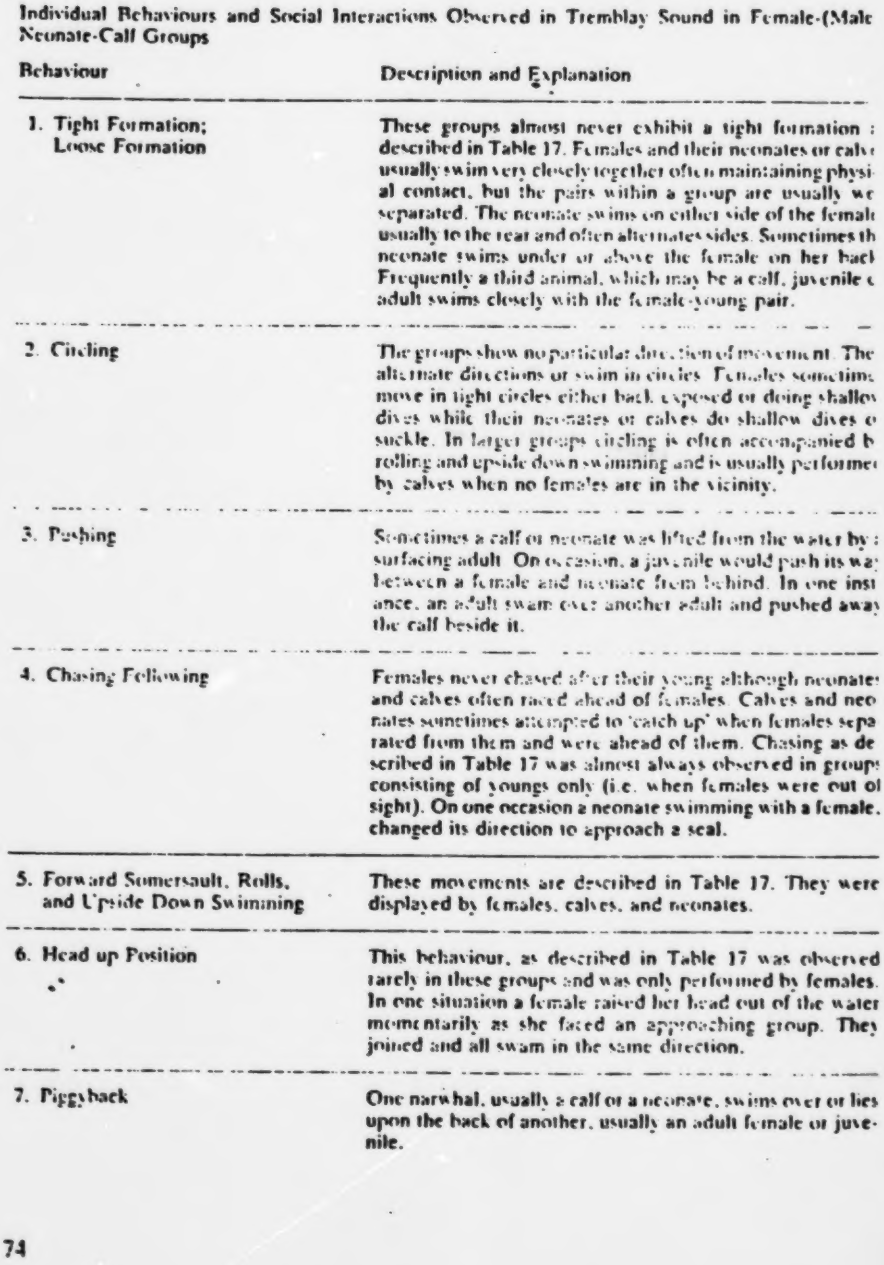


Fig. 25 a. Two male narwhals crossing their tusks over the back of a third. The latter's back emerges from the water.

b. Three male narwhals with their heads above the water, crossing their tusks.

c. Two male narwhals crossing their tusks. The male on the right is in a vertical position; only the anterior part of the tusk emerges from the water. The male on the left lies at the surface. During this behavioural display, the male on the right taps the tip of the other's tusk repeatedly with his own tusk, then emerges. (Redrawn from HELEN SILVERMAN, 1979).

The following Table (loc. cit. Table 18) describes the same behaviour in Female-(Male)-Neonate-Calf groups:



Individual Behaviours and Social Interactions Observed in Tremblay Sound in Female-(Male Neonate-Calf Groups

Behaviour	Description and Explanation
1. Tight Formation; Loose Formation	These groups almost never exhibit a tight formation : described in Table 17. Females and their neonates or calv usually swim very closely together often maintaining physi al contact, but the pairs within a group are usually we separated. The neonate swims on either side of the femal usually to the rear and often alternates sides. Sometimes th neonate swims under or above the female on her bac Frequently a third animal, which may be a calf, juvenile adult swims closely with the female-young pair.
2. Circling	The groups show no particular direction of movement. The alternate directions or swim in circles. Females sometim move in tight circles either back exposed or doing shallo dives while their neonates or calves do shallow dives suckle. In larger groups circling is often accompanied rolling and upside down swimming and is usually performe by calves when no females are in the vicinity.
3. Pushing	Sometimes a calf or neonate was lifted from the water by surfacing adult. On occasion, a juvenile would push its wa between a female and neonate from behind. In one ins ance, an adult swam over another adult and pushed awa the calf beside it.
4. Chasing Following	Females never chased after their young although neonate and calves often raced ahead of females. Calves and neonates sometimes attempted to 'catch up' when females separated from them and were ahead of them. Chasing as described in Table 17 was almost always observed in group consisting of youngs only (i.e. when females were out o sight). On one occasion a neonate swimming with a female, changed its direction to approach a seal.
5. Forward Somersault, Rolls, and Upside Down Swimming	These movements are described in Table 17. They were displayed by females, calves, and neonates.
6. Head up Position	This behaviour, as described in Table 17 was observed rarely in these groups and was only performed by females. In one situation a female raised her head out of the water momentarily as she faced an approaching group. They joined and all swam in the same direction.
7. Piggyback	One narwhal, usually a calf or a neonate, swims over or lies upon the back of another, usually an adult female or juvenile.

8. Approach	Approaching narwhals showed similar behaviour to that described in Table 17 (head on approach). Calves and neonates often approached adults from the rear. Adults sometimes turned to meet them head on. An adult male met an approaching calf in this manner.
9. Head on Caudal Peduncle	A female lifts her head and places it on the caudal peduncle of another female. She then slides back into the water.
10. Tusk-Body Contact	(a) A male rubs its tusk along back of female; calf is not involved. (b) A calf swims under a male's tusk which is raised slightly from the water surface. A male which is behind a calf continuously touches and strokes the calf on its back and caudal peduncle with its tusk. (This male may actually be a female with a tusk).
11. Suckling	(a) The female is back exposed and still or moving slowly while the neonate or calf is underwater suckling. (b) The female is back exposed and turning in tight circles, either slowly or quickly while the neonate or calf is under the surface (sometimes upside down) suckling. (c) The female is back exposed while her young has its tail at the surface and body angled downwards towards the mammary slits. (d) The young is ahead of the female. It turns and moves rapidly towards the female and strikes her at the mammary slit. (e) The female rolls onto her side and her young suckles. This was once observed performed simultaneously by two pairs. (f) The young dives and butts against the region of the mammary slits. The female sinks under the surface, onto her side and her young suckles. Her young appears to initiate suckling. (g) The female rolls upside down under the surface and her young suckles. (h) The calf nuzzles into mammary region for one sec. but the female swims on and there is no suckling. The suckling attempt by the calf is unsuccessful.
12. Young Independence	One or more neonates or calves or combination of both (sometimes with juveniles) swim together with no female in sight. The females have probably gone on a deep dive. Individuals in these groups usually swim very quickly and closely together. They chase each other and dive in circles around one another. There is a great deal of body contact. For example, flippers often are touching as two individuals swim side by side. Another common observation is when a neonate or calf leaves its mother and temporarily joins an approaching group. When there are two or more females in a group, a neonate may temporarily leave its mother and swim with another female. On two occasions, females were observed to dive deep, leaving their neonates to swim unaccompanied or with another group.

	In a group consisting of three females and three calves, there was a great deal of interaction between the calves. They often separated from the females, circled, swam together, and raced back to their mothers.
13. Bubble Blowing	This was observed rarely.

There were many variations of tusk crossing (Table 17). Some of these are illustrated in Figs. 25 a-c. Very often, when two or more males crossed tusks, a female or a young juvenile male with a very short tusk was lying horizontally between the interacting males. Juvenile males frequently crossed tusks with adults, but the younger juveniles seemed to be unable to do so because of their short tusks. However, one young juvenile male managed to cross its tusk tip with that of an adult male, above the head of an adult female. The tusk of the juvenile barely reached the adult's tusk.

It seemed that males were "careful" not to harm others with their tusks. They never rushed at each other and when approaching one another tusks were often pointed away from each other.

On some occasions during localized movements groups remained in the same general area for long time periods. The longest period that we kept track of one group of whales was 2.5 hours. This group remained within an area of about 10 to 20 m²; the animals were interacting continuously above and below the surface. During localized movements female-(male)-neonate-calf groups moved around in much larger areas than the other group types.

From a helicopter (altitude of 600 ft), it seemed that many such-groups had stopped directed movements simultaneously and were either involved in the described interactions, or were moving in various directions with no directional tendency on the whole. These groups were well spaced and formed herds about 2 km in diameter. On one occasion two herds were observed simultaneously about 3 to 4 km apart. On another occasion, while we were observing one herd, we were informed of another herd 3 to 4 km distant."

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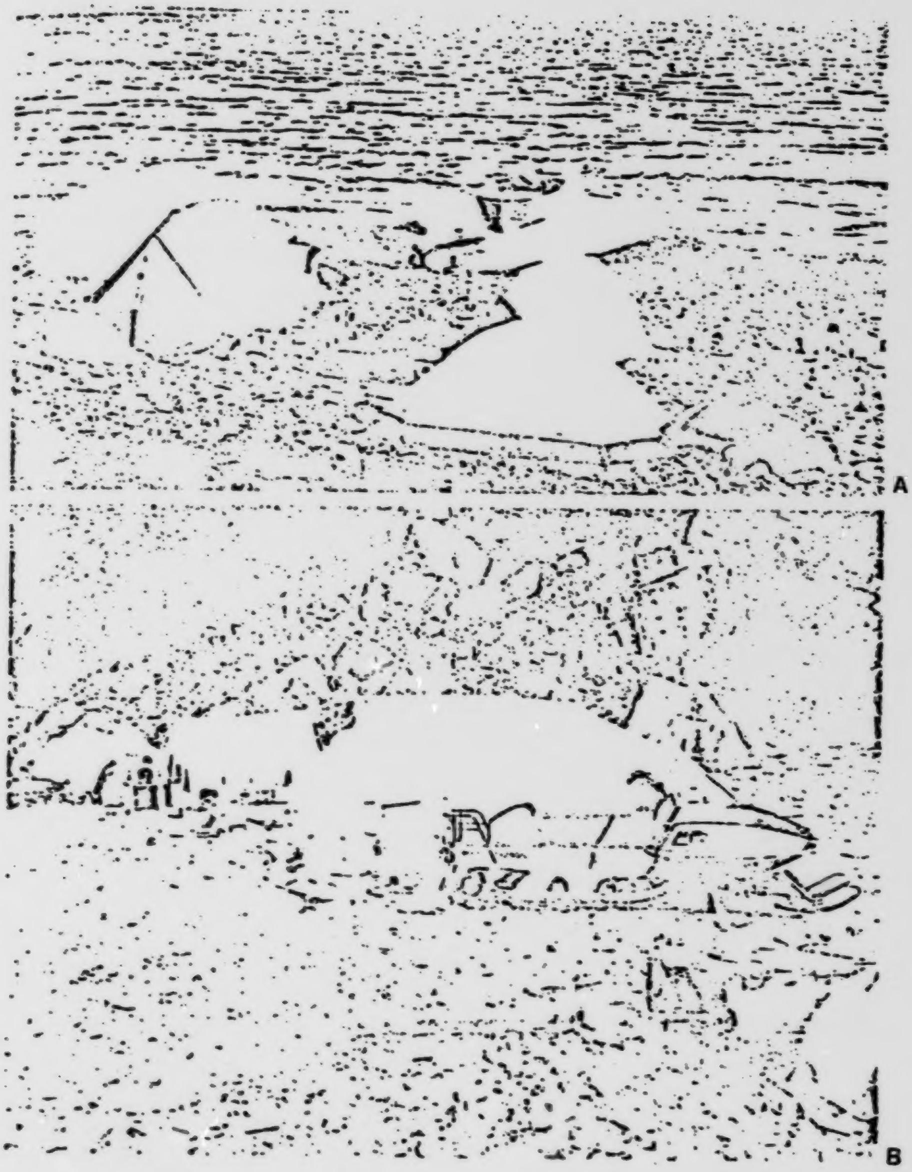
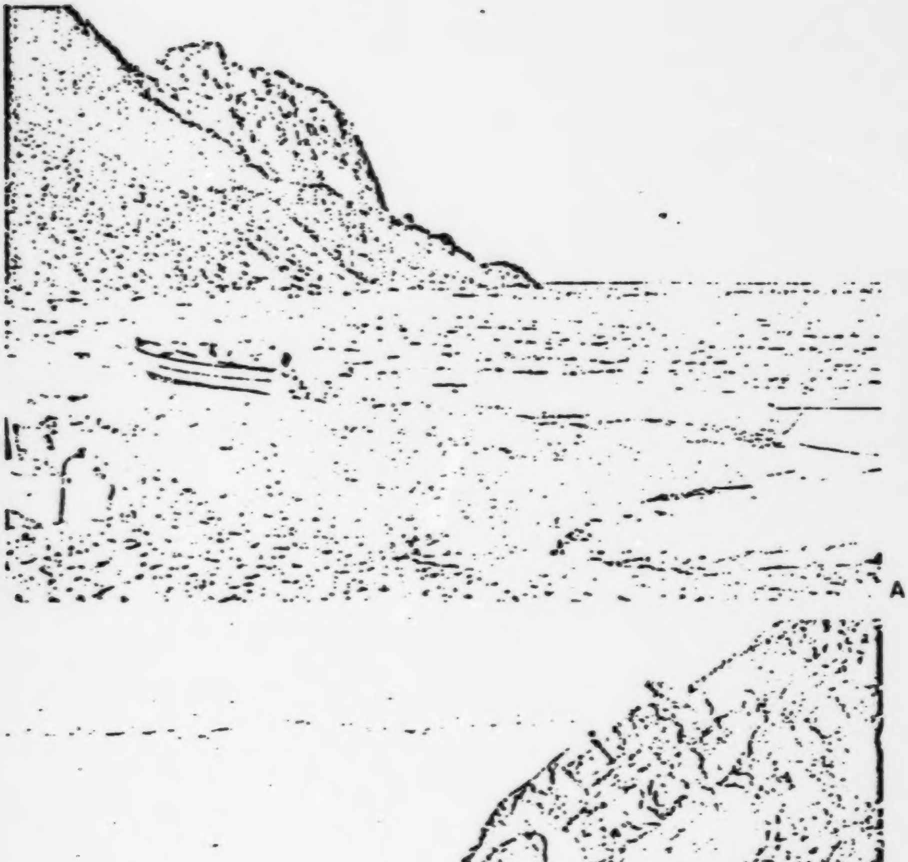
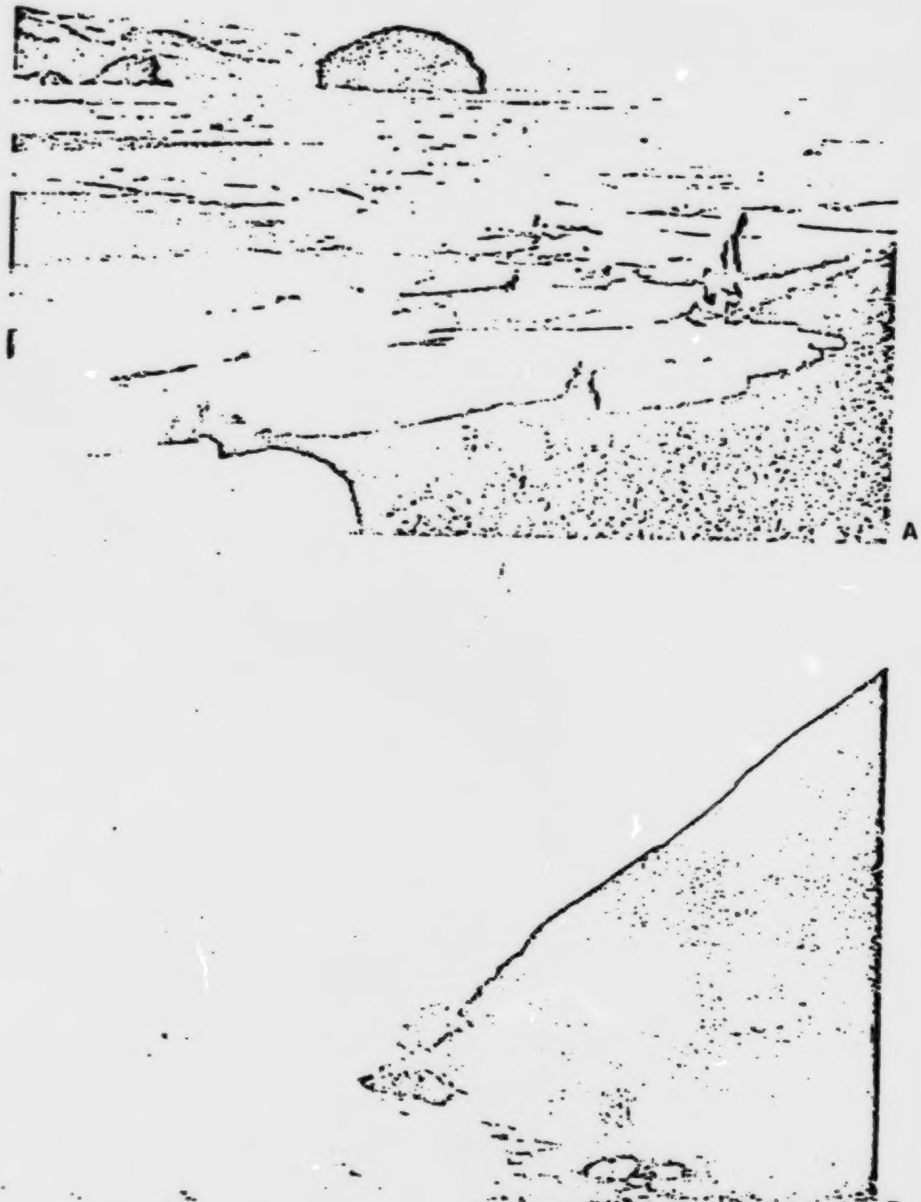


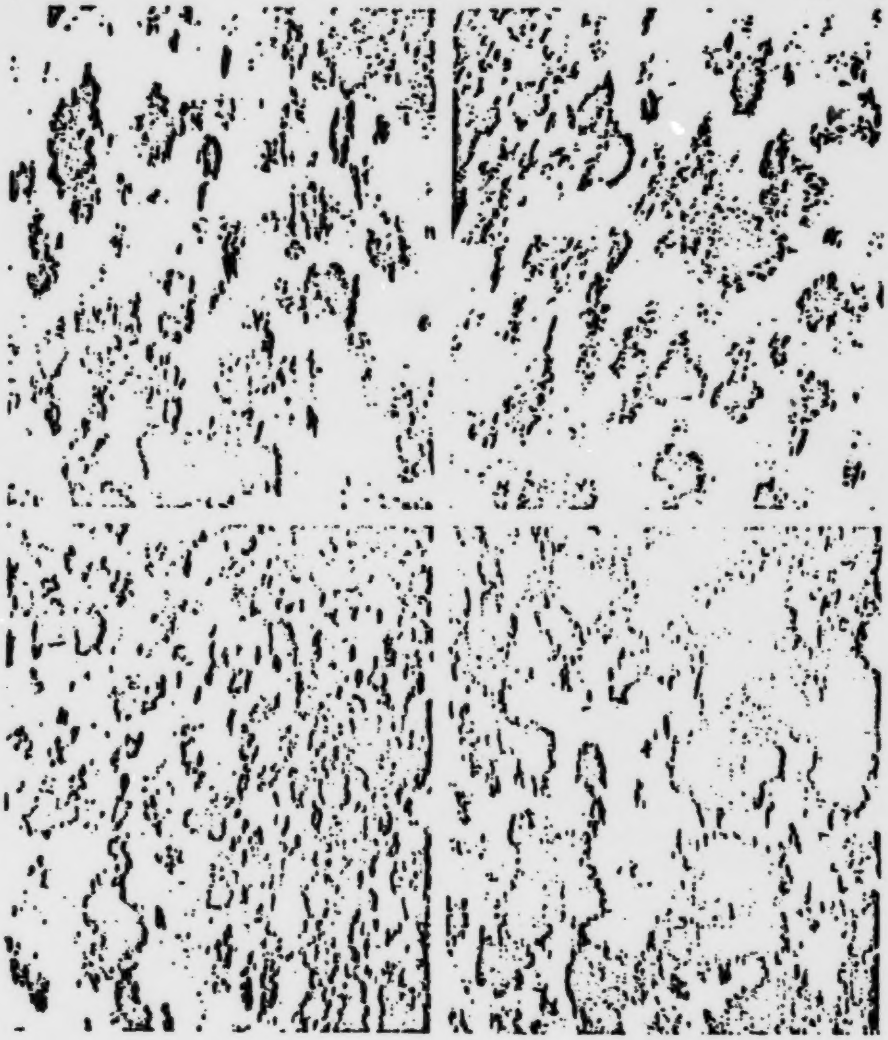
Pl. I Sadleeahrosuk Inuit camp at Pond Inlet, with (A) my own tent and (B) tents of the Inuit hunters. Japanese snowmobile in lower picture



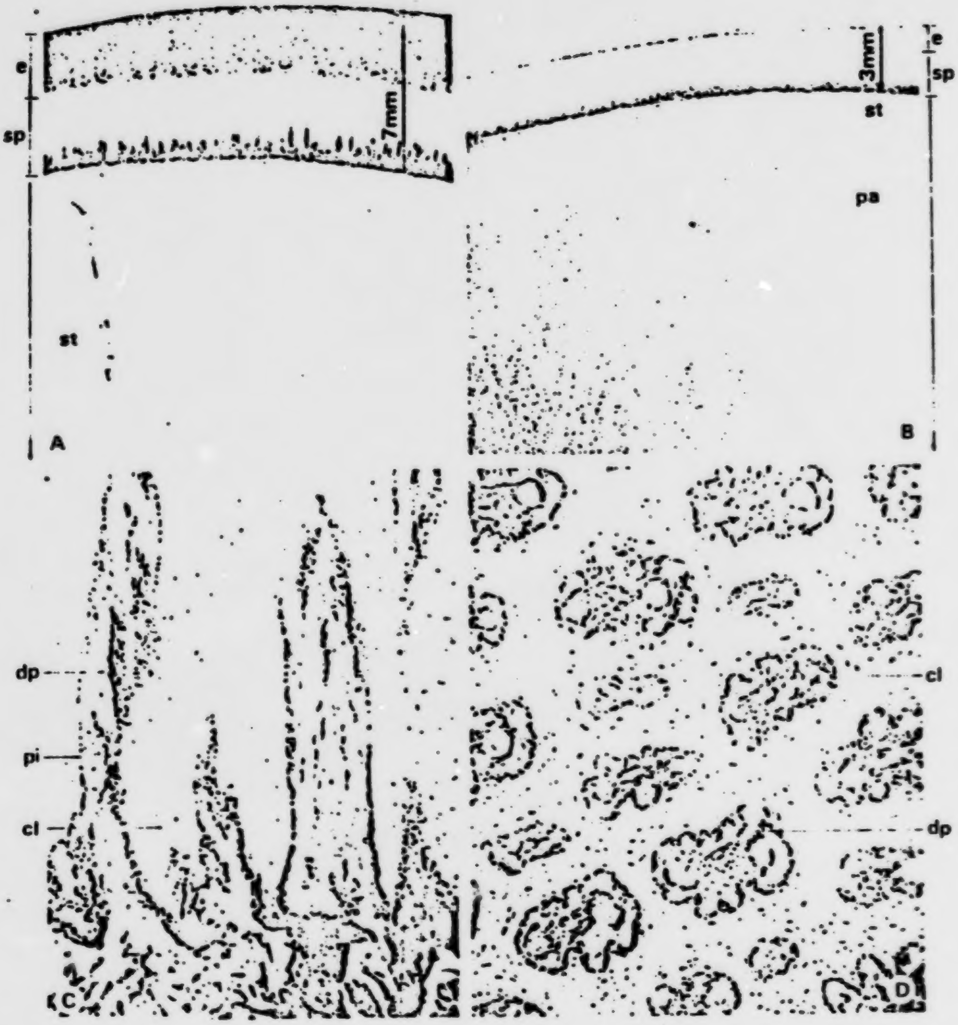
Pl. II (A) Panorama of Baffin Land coast to the West of the camp. High, primitive mountains immediately behind the camp. (B) Ice floes on Pond Inlet drifting toward Baffin Bay.



Pl. III Drift ice on Pond Inlet. (A) Bylot Island in the background. (B) High coast line, East of camp, just before Pond Inlet opens into Baffin Bay.



Pl. IV Pigmentation of the skin of the fluke of an adult, male narwhal. (No. 812; 26 7 1982)

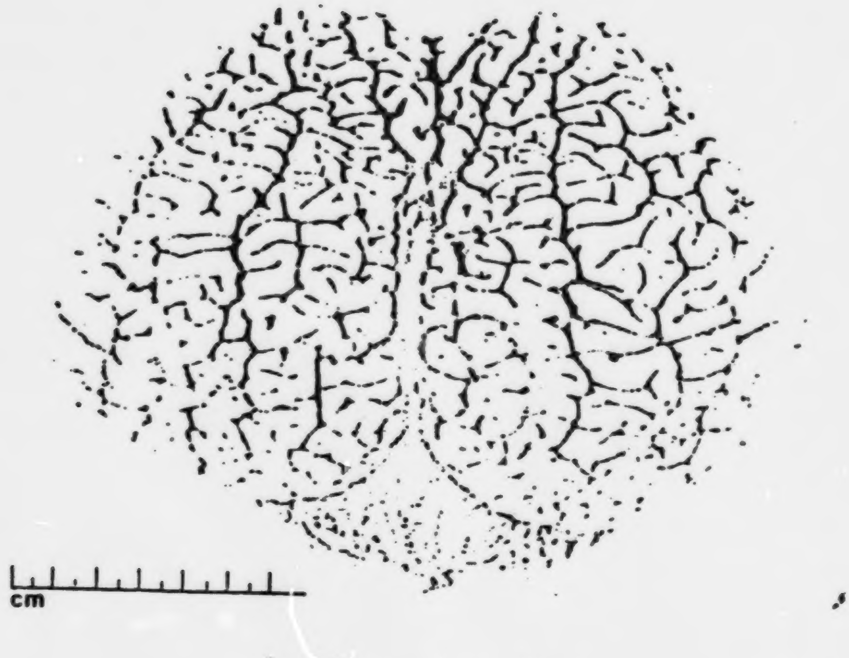


Pl. V (A) Skin of narwhal, *Monodon monoceros*, from antero-lateral aspect of melon. The corium here is very deep, and there is no panniculus adiposus. (B) Skin of *Delphinapterus leukas* from the region of the auditory meatus. (C) Magnified section of the papillary layer of the narwhal with longitudinal sections of the papillae. (D) Papillary layer with cross-sections of papillae.

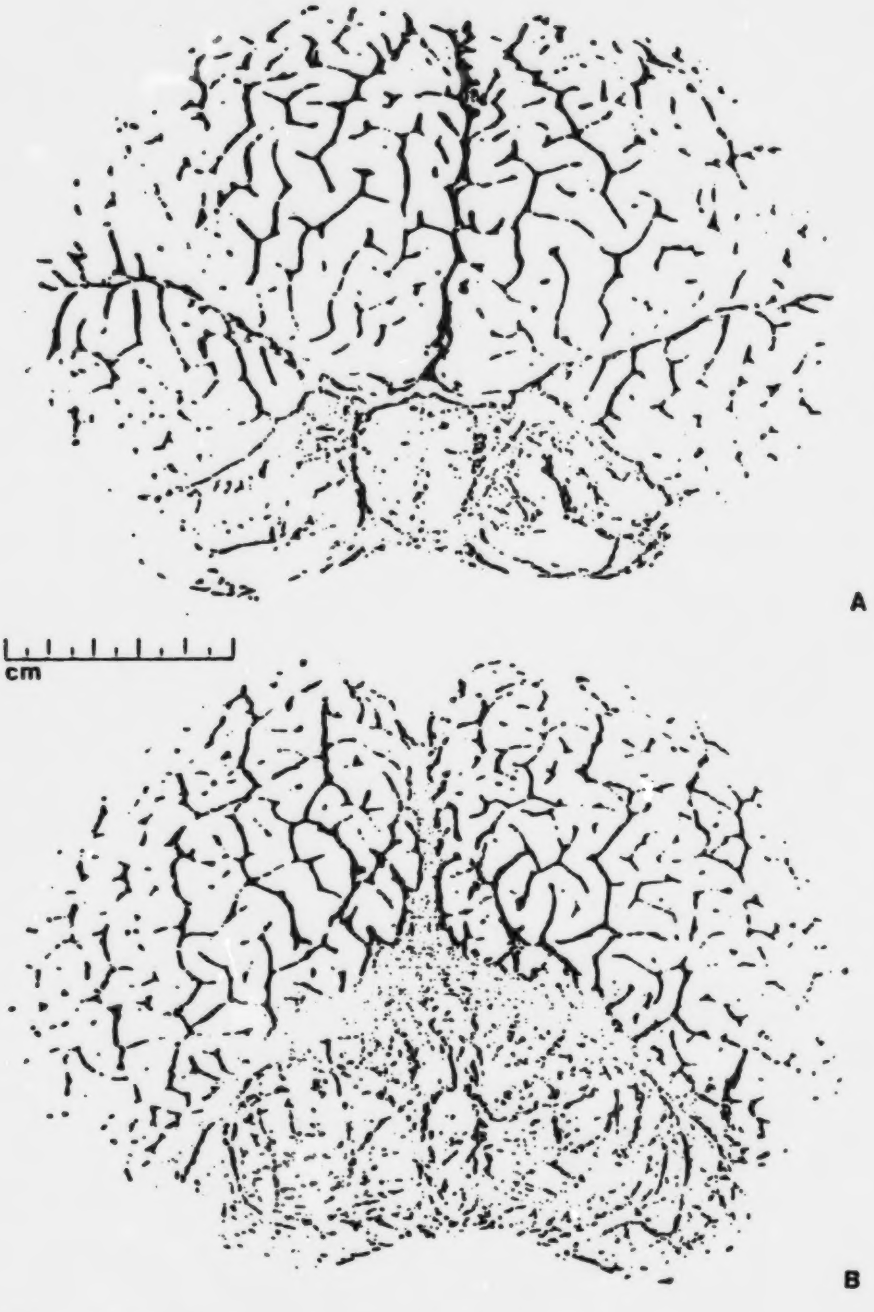
cl = dermal ridges
dp = dermal papillae
e = epidermis
pa = panniculus adiposus

pi = pigmented basal cell of epidermis
sp = papillary layer
st = corium*

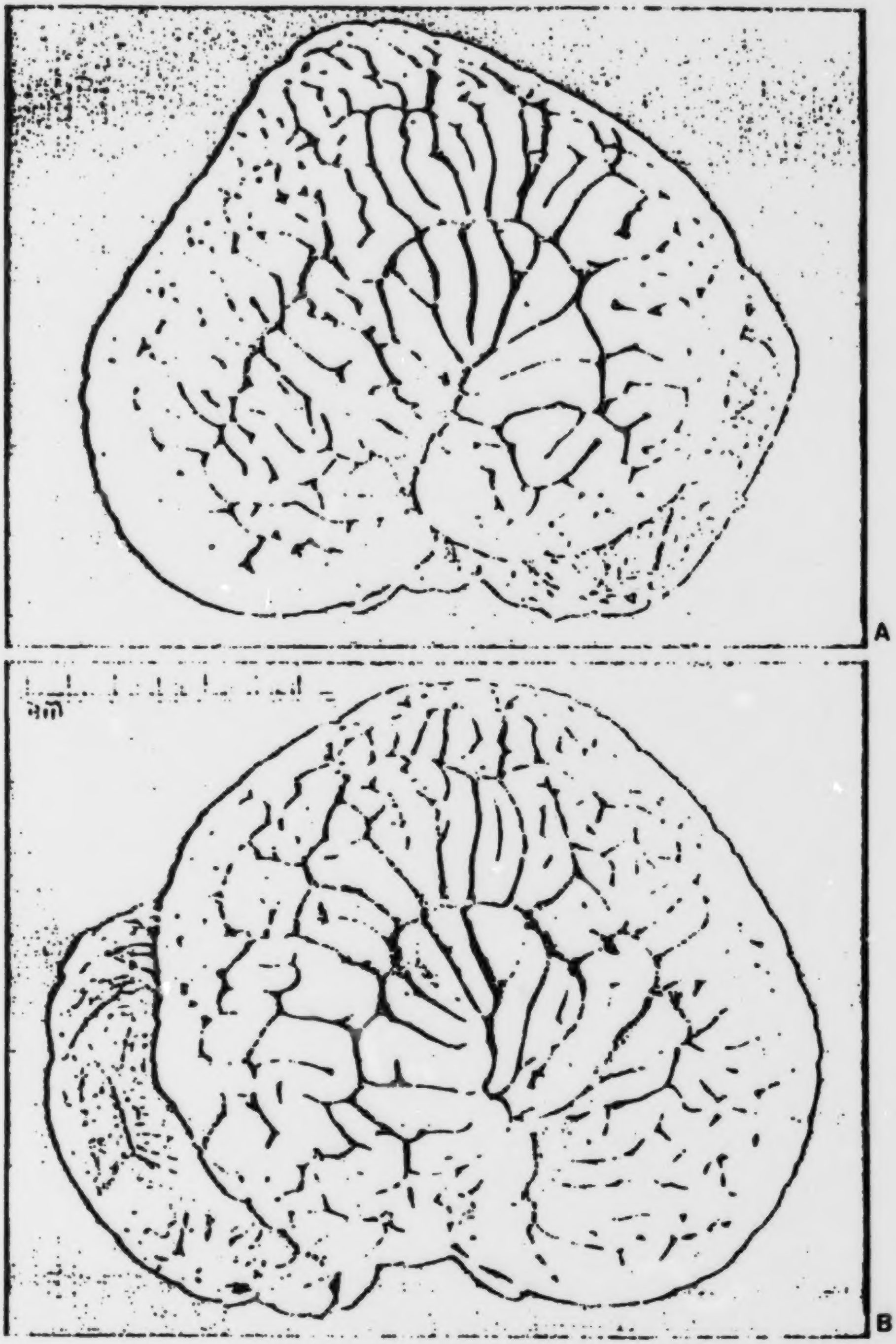
(*)(text has stratum "texticulare" which does not seem to exist. Suggest misprint for "reticulare").



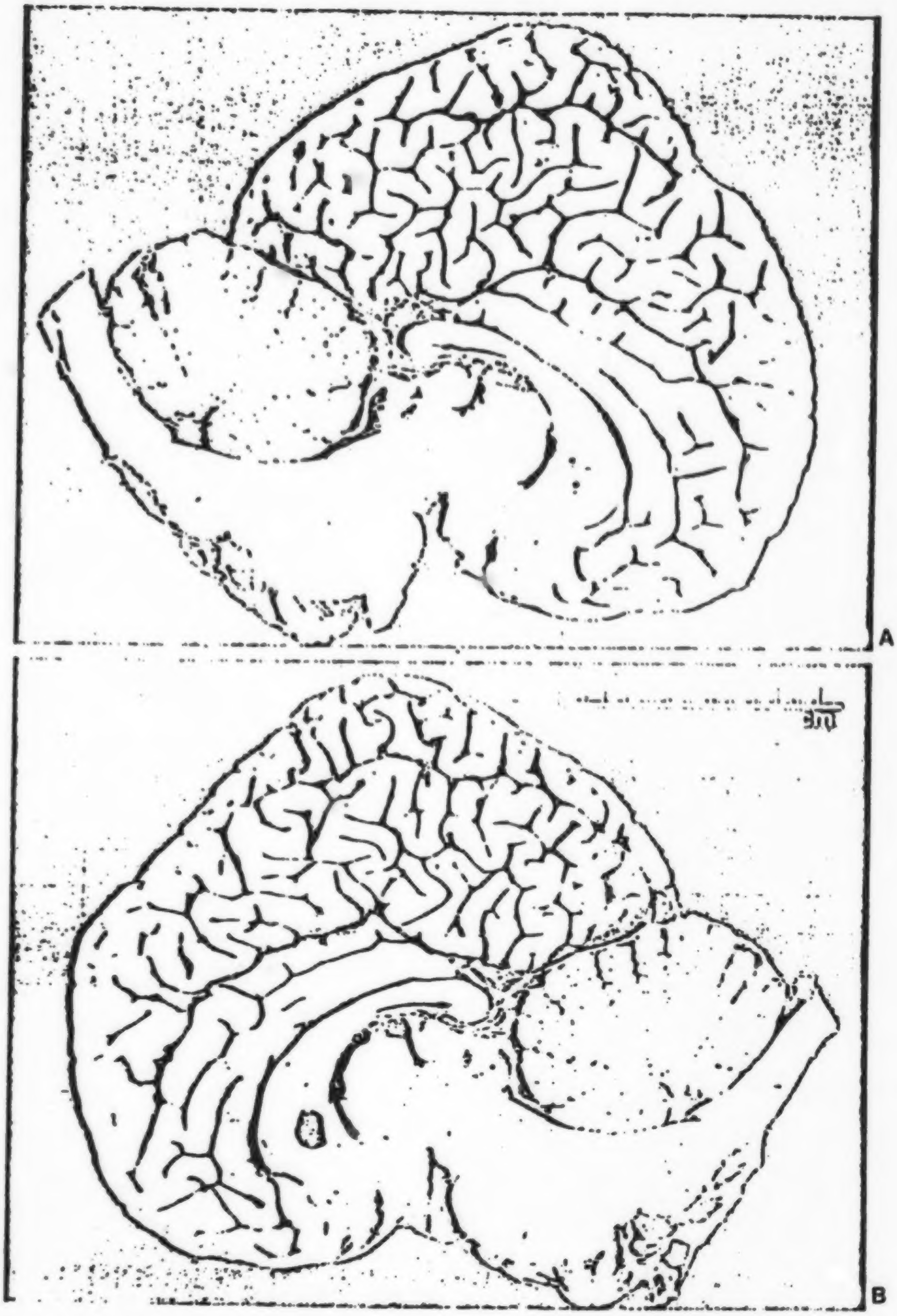
Pl. VI Photographs of (A) dorsal and (B) basal aspects of narwhal (No. 812; brain weight 2,605).



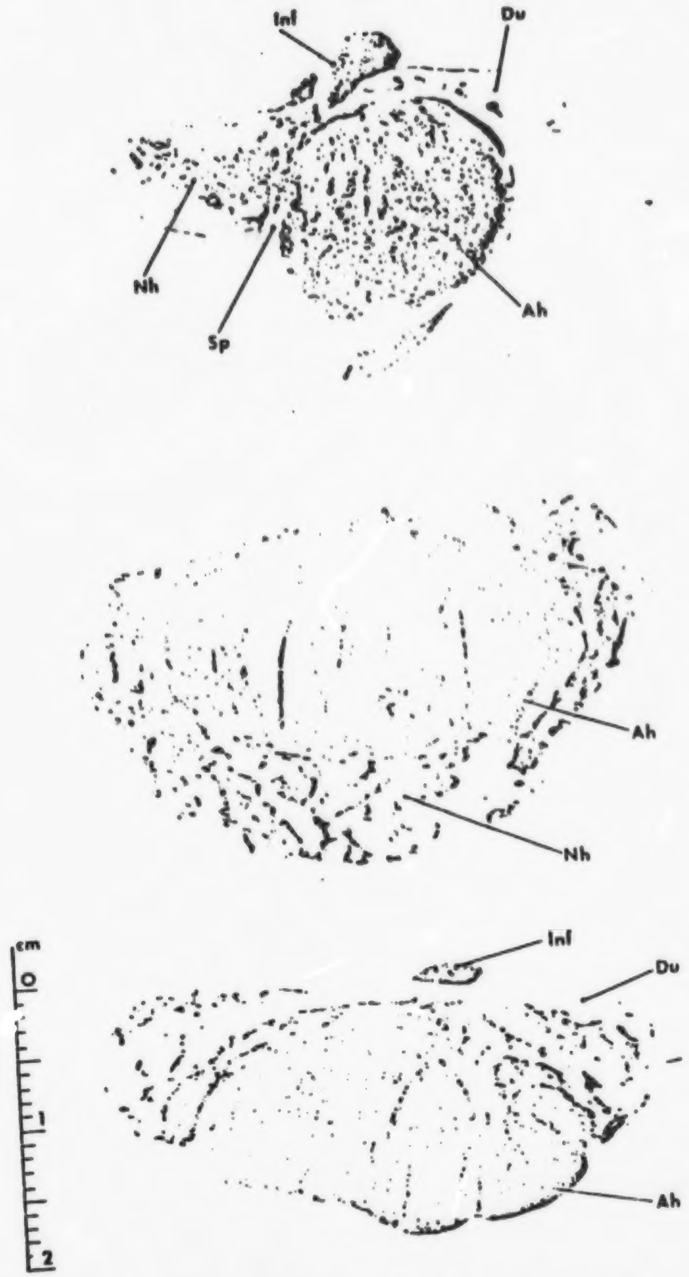
Pl. VII Photographs of (A) frontal and (B) caudal aspects of brain of narwhal (No. 812).



Pl. VIII Photographs of (A) left and (B) right lateral aspects of brain of narwhal (No. 812).

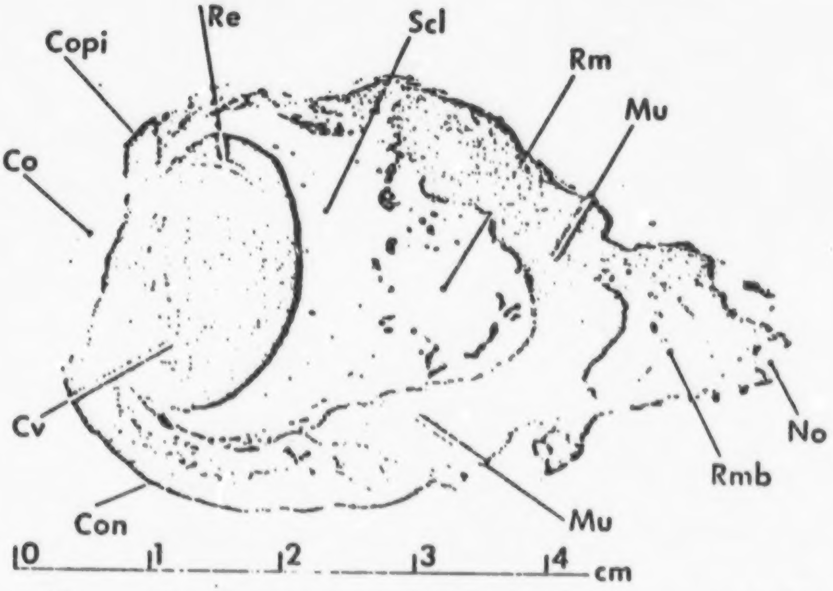


Pl. IX Photographs of medial aspects of brain of narwhal (No. 812).



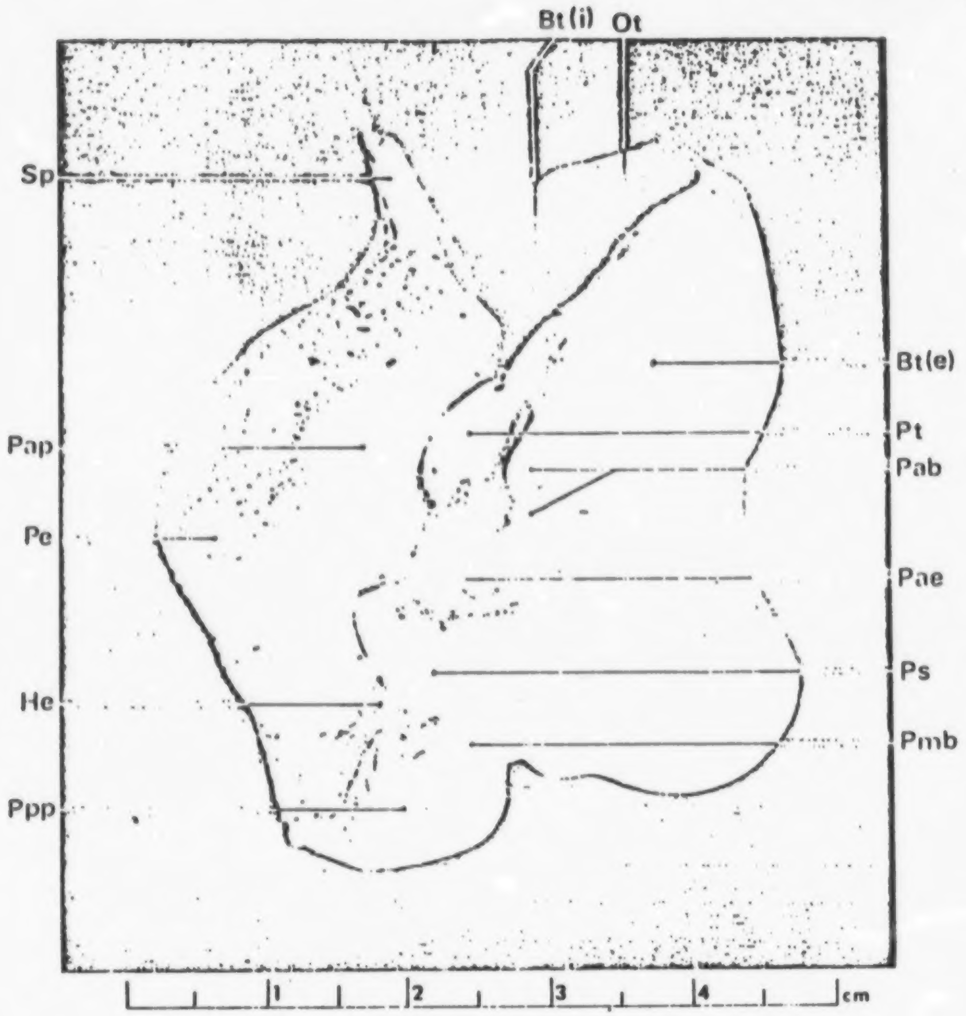
P1. X Photographs of (A) median sagittal section, (B) basal and (C) rostral views of the hypophysis of the narwhal.

Ah = anterior pituitary
Du = dura mater
Inf = infundibulum
Nh = neurohypophysis
Sp = septum from dura



Pl. XI Equatorial section through narwhal eye.

Co = cornea
Con = bulbar conjonctiva
Copi = limbus of pigmented sclera
Cv = vitreous humour
Mu = muscles of eye.
No = optic nerve
Rmb = connective tissue envelope around ret
of optic nerve
Re = retina
Rm = rete mirabile
Scl = sclera

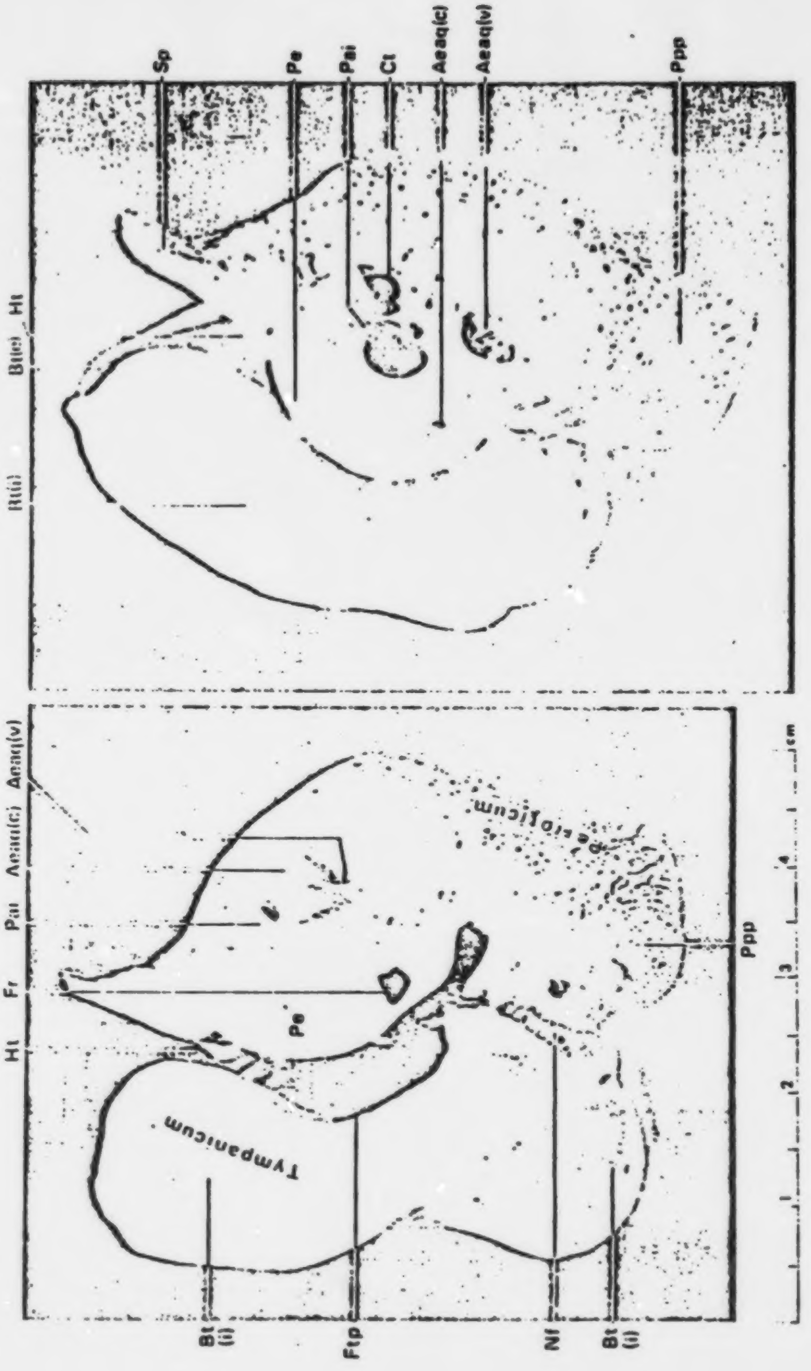


Pl. XII Tympano-periotic region ofadult narwhal, meatal aspect.

Bt(e) = tympanic cavity (outer wall)
Bt(i) = tympanic cavity (inner wall)
He = epitympanic recess
Ot = opening of Eustacian tube into tympanic cavity
Pab = anterior process of bulla
Pae = external opening of (bony) acoustic meatus
Pap = anterior process of petrosal bone
Pe = petrosal bone
Pmb = median process of tympanic bulla
Ppp = posterior (mastoid) process
Ps = sigmoid process
Pt = tubal process
Sp = suprameatal spine

Pl. XIII Tympano-periotic bones of an adult narwhal; visceral aspect.

Aeaq (c) = outer opening of cochlear aqueduct
Aeaq (v) = outer opening of vestibular aqueduct
Bt(e) = tympanic cavity (outer wall)
Bt(i) = tympanic cavity (inner wall)
Ct = transverse crest
Fr = round window
Ftp = tympanic fissure
Ht = tympanic hiatus
Nf = canal for facial nerve
Pai = internal opening of acoustic meatus
Pe = petrosal bone
Ppp = posterior (mastoid) process
Sp = suprameatal spine


Sp
Pe
Pai
Ct
Aeaq(c)
Aeaq(v)
Ppp
Bt(e)
Ht
Bt(i)
Aeaq(v)
Aeaq(c)
Aeaq
Pai
Fr
Ht
Pe
Tympanicum
Perioticum
Ppp
Bt (i)
Ftp
Nf
Bt (i)
1
2
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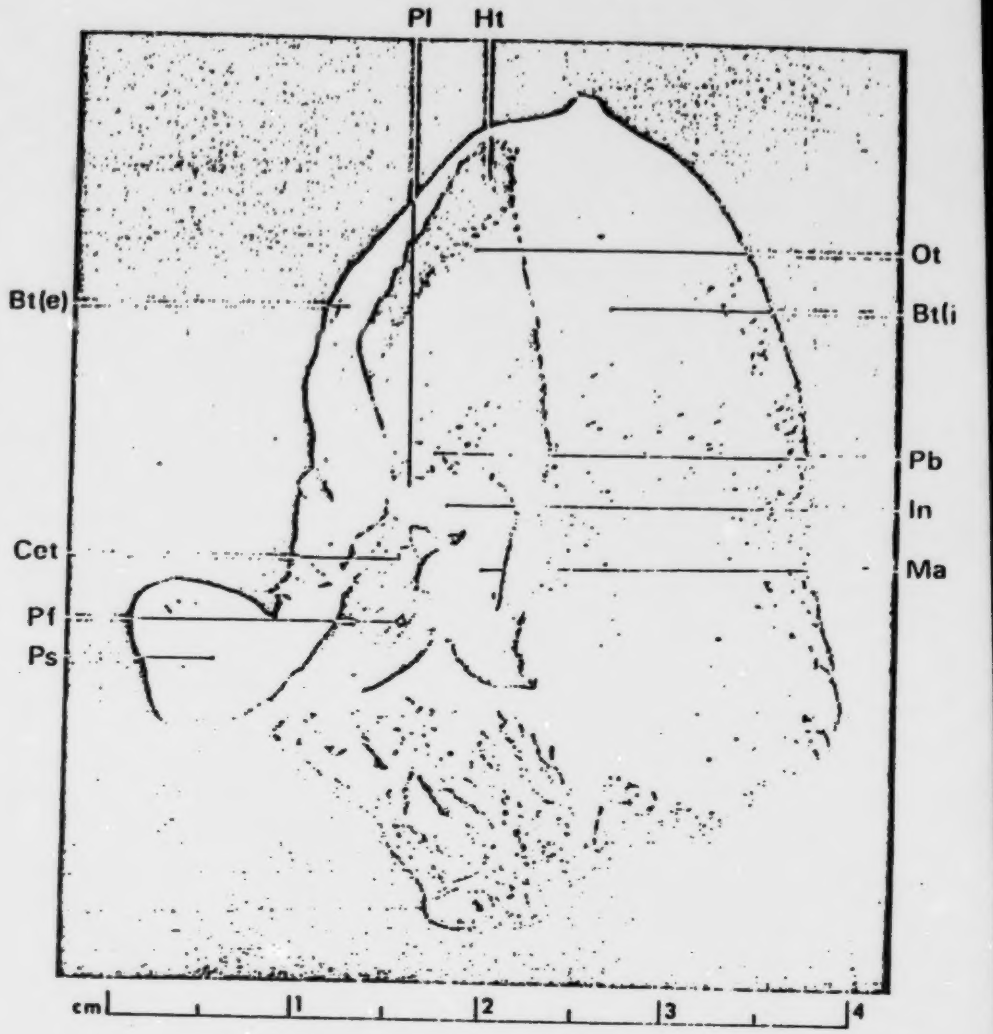
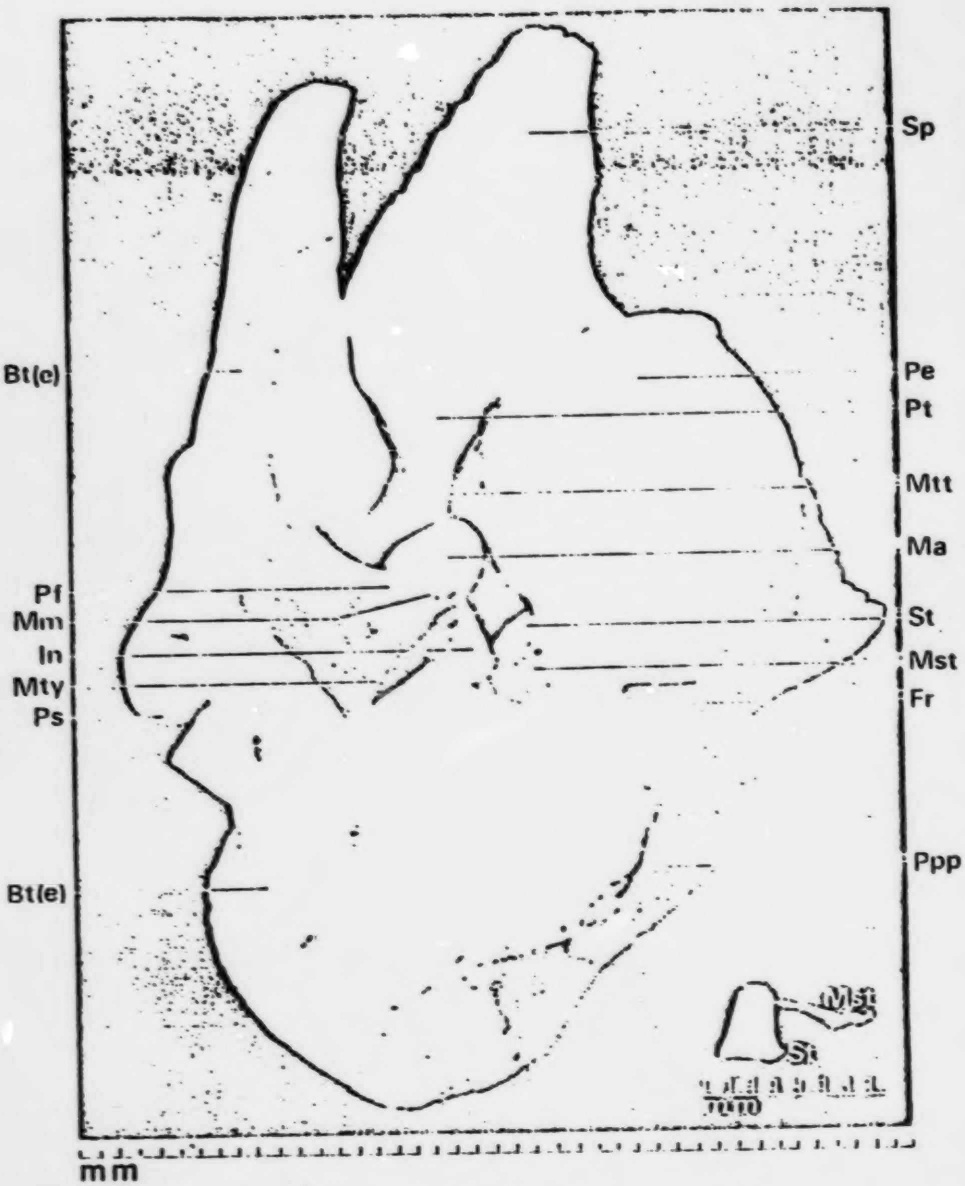
cm



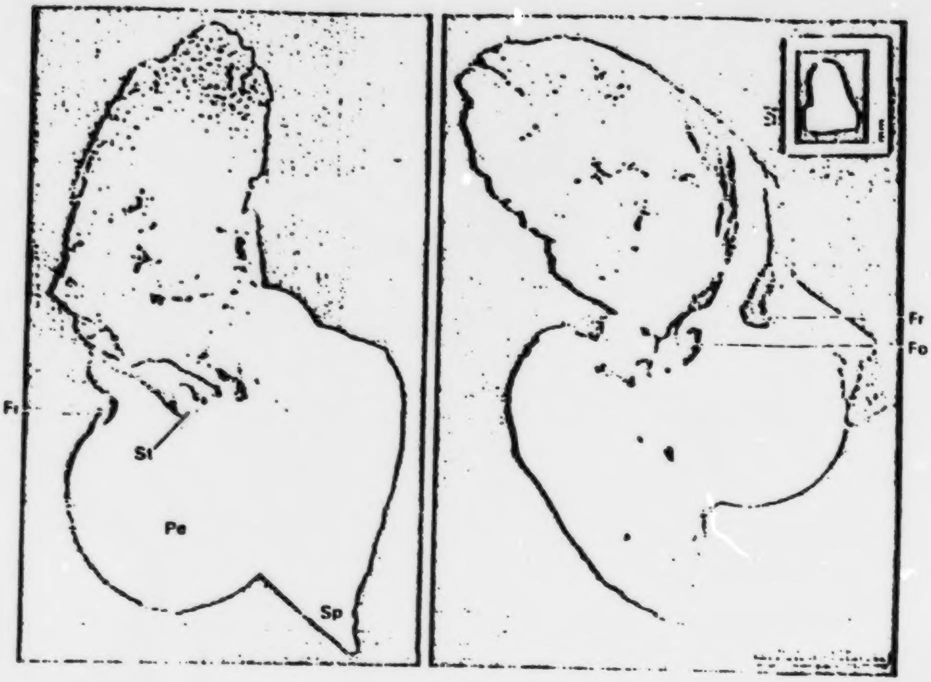
Pl. XIV Tympanic cavity of foetal narwhal with malleus and incus *in situ*

Bt(e) = tympanic cavity (outer wall)
Gst = articulation surface for stapes
In = incus
Ma = malleus
Ot = tympanic opening of Eustachian tub
Pb = short crus of incus
Ps = sigmoid process



Pl. XV Interior aspect of tympanic cavity with ossicles *in situ*, after removal of wall of tympanicbulla

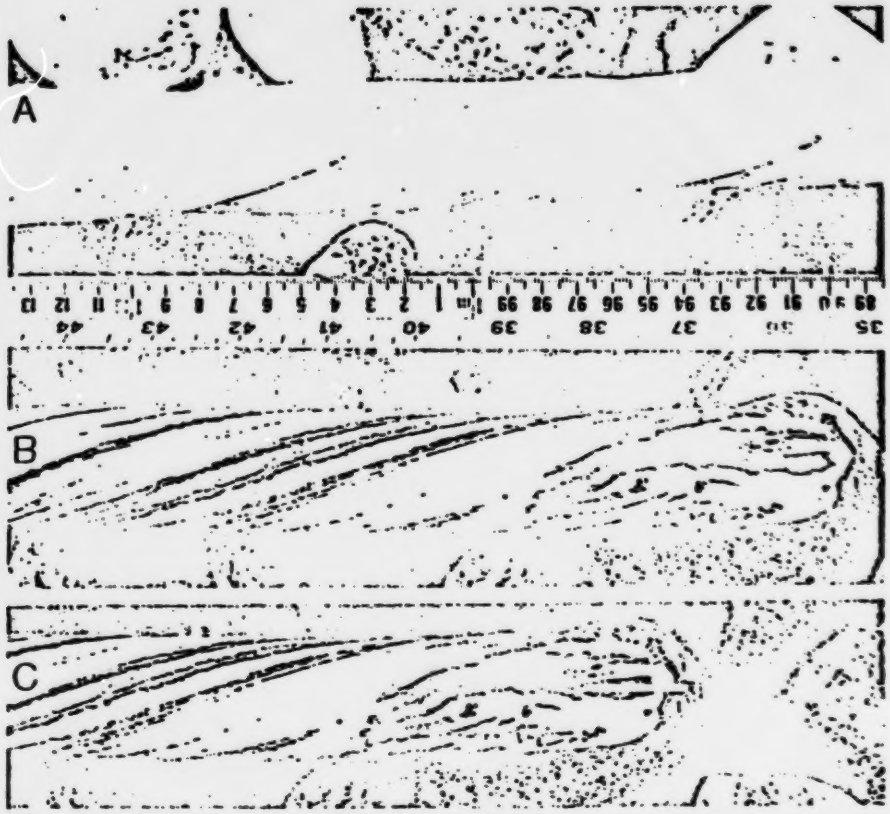
Bt(e) = Outer wall of tympanic bulla
Fr = round window
In = incus
Ma = malleus
Mm = manubrium of malleus
Mst = stapedius muscle (dessicated)
Mtt = tensor muscle of tympanum
Mty = tympanic membrane (dessicated)
Pe = petrosal bone
Pf = Folius' process
Ppp = posterior (mastoid) process
Ps = sigmoid process
Pt = tubal process
Sp = suprameatal spine
St = stapes



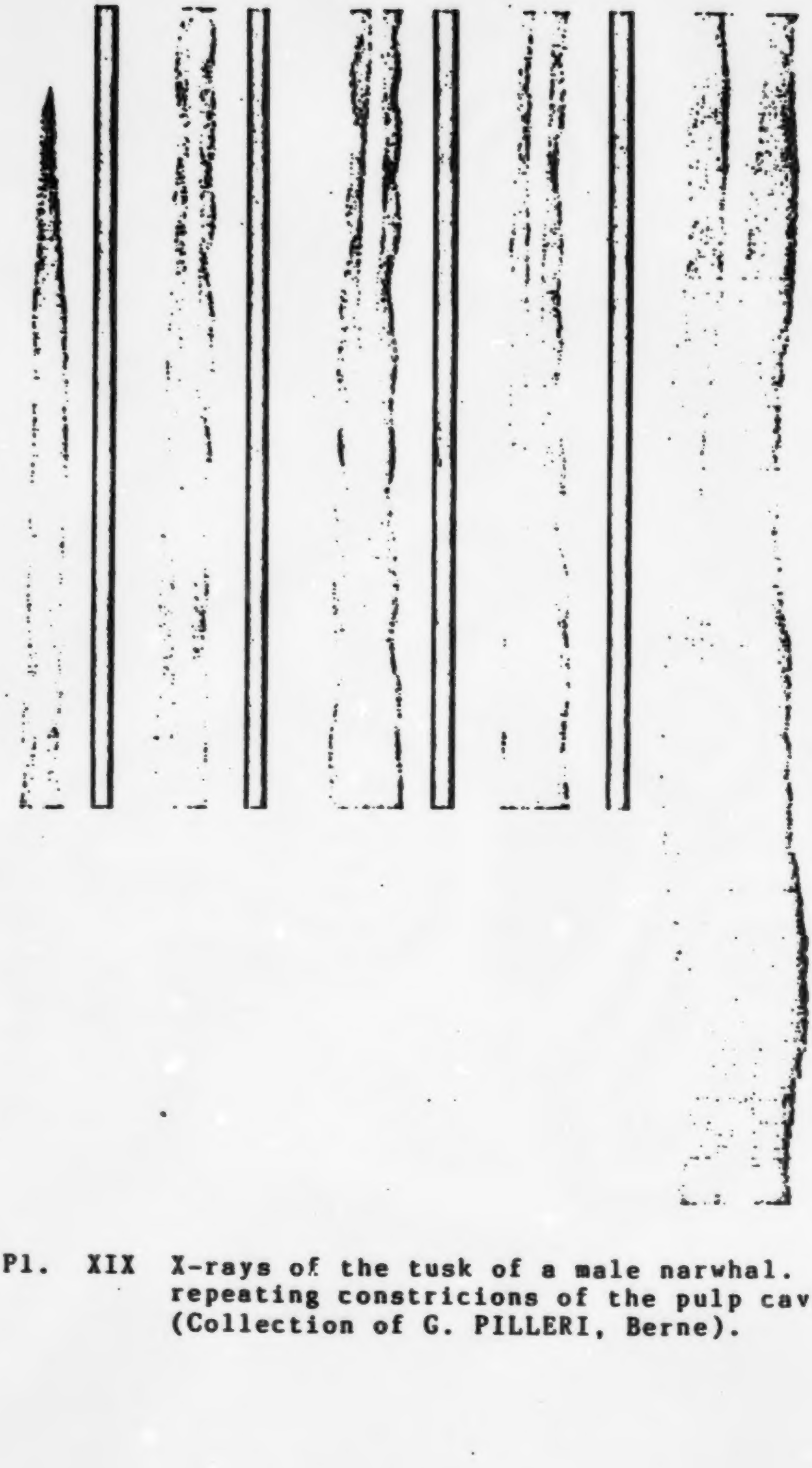
Pl. XVI Petrosal bone of an adult narwhal, seen from the tympanic cavity. Detail of stapes (St): (A) in situ; (B) removed. (Scale in mm).

Fo = oval window
Fr = round window
Pe = petrosal bone
Sp = suprameatal spine

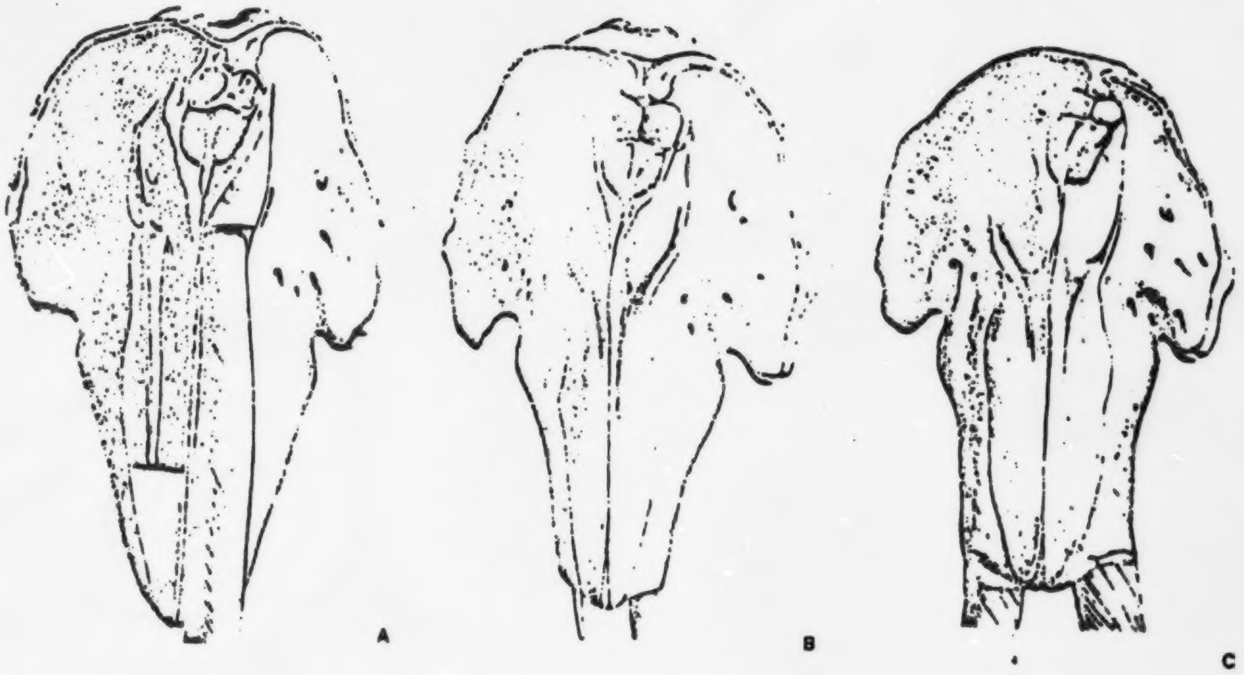
Pl. XVII Tusk of a male narwhal caught in Pond Inlet, Baffin Land on 26 7 1982. (Collection of G. PILLERI, Berne).



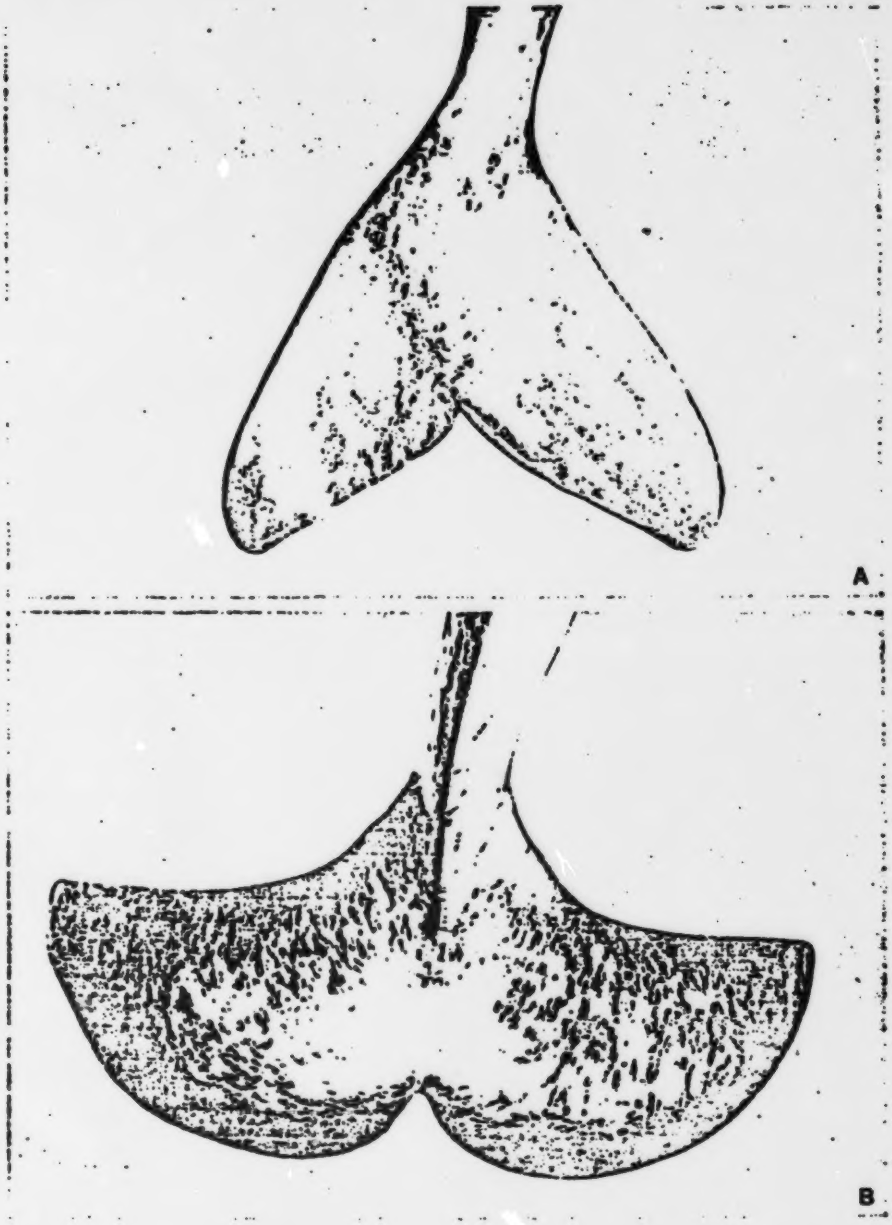
Pl.XVIII (A) Middle section of a tusk; (B) tip of a broken-off tusk. Note the algae-covered abrasion and (C) the pulp cavity. Specimens from Pond Inlet, Baffin Land, Summer of 1982.



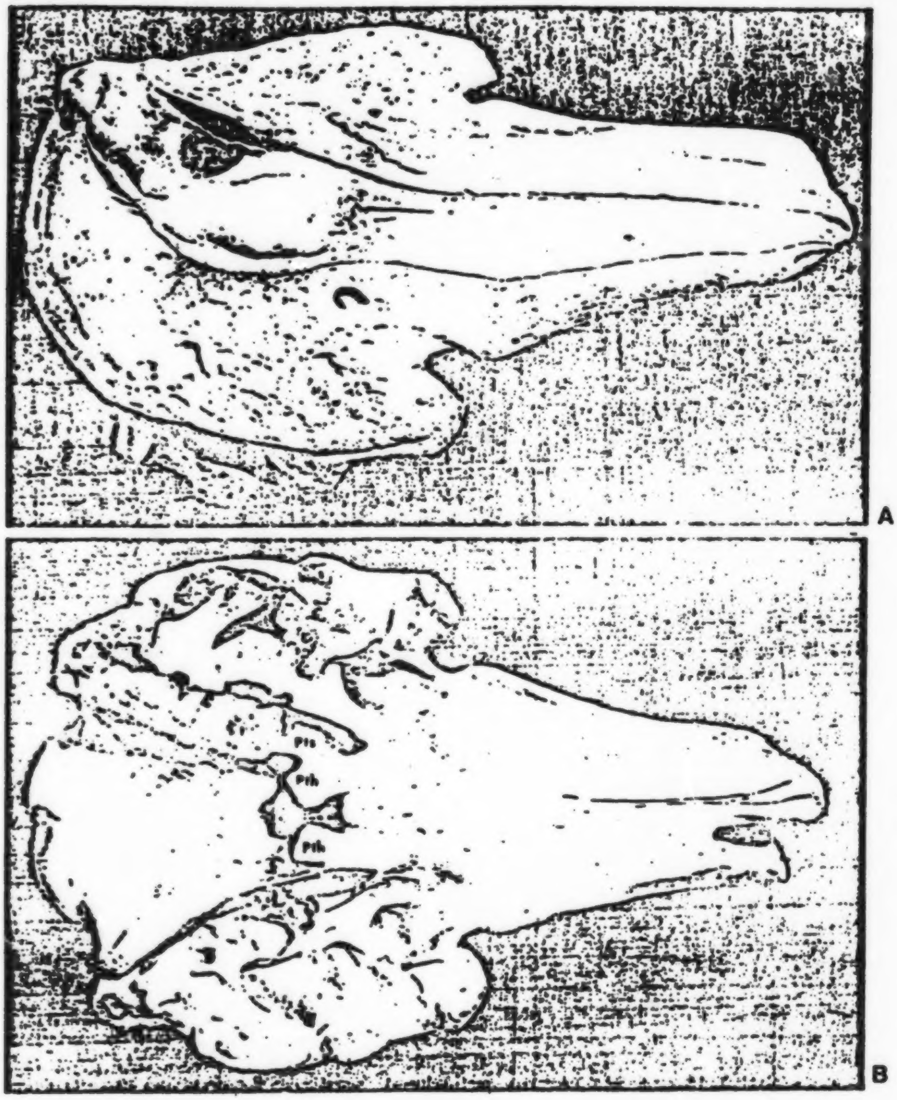
Pl. XIX X-rays of the tusk of a male narwhal. Note the repeating constricions of the pulp cavity. (Collection of G. PILLERI, Berne).



Pl. XX (A) Dissection of a left, fully developed and a right, undeveloped, tusk of a male narwhal. (B) juvenile and (C) adult two-tusked males (after VAN BENEDEN and GERVAIS, 1880.



Pl. XXI Photographs of dorsal aspect of flukes from (A a full-term foetus and (B) an adult narwhal. The scales of the two photographs are not the same. The specimens were narwhals taken in Pond Inlet in the summer of 1982.



Pl. XXII There is, between the two pterygoid hamuli (Pth), a bone- and air-free space which is flanked by the pterygoid sinuses (Pts). This pterygoschisis makes it possible for sounds produced in the larynx to be propagated in a ventrad direction.